Volume LXXI Number

THE BOTANICAL GAZETTE

Editor: JOHN M. COULTER

JUNE 1921

Chemical Changes in Wheat during Germination. Contributions from the Hull Botanical Laboratory 281 - - - - - - Helen A. Choate 409
(With Plate XVIII and two figures)

Undescribed Willows of the Section Cordatae - - Carleton R. Ball 426
(With one figure)

Vessels of the Gnetalean Type in Angiosperms - - R. C. MacDuffie 438
(With Plates XXIX–XXXII)

Embryogeny and Sporogenesis in Reboulia hemisphaerica Arthur W. Haupt 446
(With Plate XXXIII and eleven figures)

Diameter Growth in Box Elder and Blue Spruce - - C. F. Korstian 454
(With three figures)

Briefer Articles
Alfred Gabriel Nathorst - - - - - - - A. C. Seward 462
(With portrait)

Current Literature
Notes for Students - - - - - - - - - - - - 466

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EDITED BY

JOHN M. COULTER

With the assistance of other members of the botanical staff of the University of Chicago

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By

JOHN M. COULTER

Head of the Department of Botany in the University of Chicago

and

MERLE C. COULTER

Instructor in Plant Genetics in the University of Chicago

THIS book has been written to meet an increasing need among botanical students. Such students in these days, in whatever phase of botany they may be specializing, find it necessary to read with understanding much of the literature of plant genetics, because it is becoming increasingly significant in all botanical problems. This means that teachers and investigators must be able to command the literature of plant genetics, much of which has been so complex as to be a closed book for the uninitiated. *Plant Genetics* is an attempt to open this subject to botanical students.

¶ The book is not intended to be a thorough, authoritative text, but a relatively simple presentation of the more significant investigations on plant genetics which will initiate the student into the subject. Material dealing with some highly specialized phases of genetics and material that is very complex have been purposely omitted for pedagogical reasons. In short, the book is an easy introduction to plant genetics.

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TABLE OF CONTENTS

		PAGE
Physiological and morphological correlations in herbaceous Angiosperms (with plates I–VII and four figures)	*E. C. Jeffrey* and *R. E. Torrey*	1
After-ripening and germination of *Juniperus* seeds. Contributions from the Hull Botanical Laboratory **275** (with one figure)	*Dean A. Pack*	32
Gametophyte and sex organs of *Reboulia hemisphaerica*. Contributions from the Hull Botanical Laboratory **276** (with twenty-one figures)	*Arthur W. Haupt*	61
A chemical and physiological study of mottling of leaves. Contributions from the Hull Botanical Laboratory **277** (with six figures)	*F. M. Schertz*	81
Gametophytic development of blister rusts (with four figures)	*J. F. Adams*	131
Development of head and flower of *Dipsacus sylvestris*. Contributions from the Hull Botanical Laboratory **278** (with fourteen figures)	*Hilary S. Jurica*	138
Reserve food materials in vegetative tissues	*Gwynethe M. Tuttle*	146
Leaf spots of the elm (with plates VIII–X and one figure)	*L. E. Miles*	161
Influence of environment on sexual expression in hemp (with plate XI and one figure)	*John H. Schaffner*	197
Experimental investigations on birch and oak (with plates XII–XV and four figures)	*Edith S. Whitaker*	220
Effect of light on germination of light-sensitive seeds. Contributions from the Hull Botanical Laboratory **279**	*Wright A. Gardner*	249
Ecology of *Tilia americana*. II. Comparative studies of the foliar transpiring power (with ten figures)	*James E. Cribbs*	289

PAGE

The vessel in seed plants (with plates XVI–XX) - *Mary C. Bliss* 314

A convenient thermoregulator (with two figures) *Heinrich Hasselbring* 327

Dormancy and hardiness in the plum. Contributions from the Hull Botanical Laboratory 280 (with four figures) - - - - - - *P. D. Strausbaugh* 337

Evolution of zoocecidia (with plates XXI, XXII) - *B. W. Wells* 358

The gametophytes of *Equisetum laevigatum* (with plates XXIII, XXIV, and three figures) - - *Elda R. Walker* 378

Comparison of development in dodder and morning glory (with plates XXV–XXVII) - - - *Gertrude E. Macpherson* 392

Chemical changes in wheat during germination. Contributions from the Hull Botanical Laboratory 281 (with plate XXVIII and two figures) - - - - - - - - - - *Helen A. Choate* 409

Undescribed willows of the section Cordatae (with one figure) - - - - - - - - - *Carleton R. Ball* 426

Vessels of the Gnetalean type in Angiosperms (with plates XXIX–XXXII) - - - - - - *R. C. MacDuffie* 438

Embryogeny and sporogenesis in *Reboulia hemisphaerica* (with plate XXXIII and eleven figures) - - - - - - - - - - *Arthur W. Haupt* 446

Diameter growth in box elder and blue spruce (with three figures) - - - - - - - - *C. F. Korstian* 454

BRIEFER ARTICLES—

Biographical sketch of Wilhelm Pfeffer (with portrait) - - - - - - - - - - *F. C. Newcombe* 152

Biographical sketch of John Macoun (with portrait) *Theo. Holm* 236

Biographical sketch of William Harris (with portrait) - - - - - - - - - - *D. S. Johnson* 331

Simple device for weighing seeds (with one figure) - *Karl Sax* 399

Use of chloroiodide of zinc in plant histology - - *Ernst Artschwager* 400

Biographical sketch of Alfred Gabriel Nathorst (with portrait) - - - - - - - - - - *A. C. Seward* 462

PAGE

CURRENT LITERATURE - - - - - - 75, 155, 238, 334, 401, 466

For titles of book reviews see index under author's name and reviews

Papers noticed in "Notes for Students" are indexed under author's name and subjects

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DATES OF PUBLICATION

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ERRATA

VOL. LXX

P. 399, line 4 from bottom, for **"trichostigmae"** read **"trichostigmatis"**

VOL. LXXI

P. 67, line 2, for "(fig. 8)" read "in the superficial portion of the antheridium"
P. 67, line 13, for "Fig. 8" read "Fig. 7"
P. 67, line 14, after "*Reboulia*" add "but fig. 8 indicates that the sequence may be irregular"
P. 67, last line, for "appears" read "walls appear"
P. 116, line 12, for "carotin" read "carotin / xanthophyll"
P. 137, line 16, for "3" read "2"
P. 255, line 8 from bottom, omit "108 *N. affinis*"
P. 323, line 11 from bottom, for "*Gnetum*" read "*Gnetum Gnemon*"
P. 339, line 12, for "are" read "is"
P. 348, line 2 of legend, for "acids" read "acid"
P. 349, line 4 of legend, for "C" read "O"
P. 357, citation 8, for "ber" read "Über"

VOLUME LXXI NUMBER 6

THE
BOTANICAL GAZETTE

JUNE 1921

CHEMICAL CHANGES IN WHEAT DURING GERMINATION

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 281

HELEN A. CHOATE

(WITH PLATE XXVIII AND TWO FIGURES)

Introduction

The subject of germination has received much attention of late, and the literature is extensive. In general, however, investigations have been directed toward two phases of the subject: (1) the external factors necessary for and affecting germination, and (2) the chemical changes occurring within the various parts of the seed during the process. The earlier investigations of this second phase, to which fuller reference will be made later, dealt directly with the chemical changes occurring within endosperm or storage substances of the embryo as germination advanced; but as a rule each of these studies has been limited to the consideration of some one substance, and hardly any two investigations have dealt with the same kind of plant. More recent work bearing upon chemical phenomena has been directed toward the problem of delayed germination. The results as summarized by CROCKER (**8**) show that in most cases this delay is due either to conditions existing within the seed coat, or to a morphological or physiological immaturity within the embryo, leading in the latter case to phenomena of after-ripening. This investigation is an attempt to determine somewhat more comprehensively the principal chemical

changes occurring in a single kind of normally germinating seed, and thus to contribute to the facts of germination in general, and at the same time to provide a possible basis of comparison for some of the still unsolved problems of delayed germination and after-ripening.

Historical

DETMER (9) in 1880 presented a comprehensive summary of the work done up to that time by himself and others on the physiology of germination, and in the section dealing with the metabolism of storage substances he outlined the general facts in regard to the appearance, in various parts of the embryo, of starch, sugar, and nitrogenous compounds following the breaking down of reserve substances. BROWN and MORRIS (5), working on barley, found that the first visible change is the appearance of starch in the embryo, and localized the secretion of diastase in the epithelial cells of the scutellum. They also stated that the endosperm is a dead tissue incapable of self-depletion, although a few years later, after further work, BROWN and ESCOMBE (4) concluded that the aleurone layer is a living tissue by whose activity depletion of the endosperm might occur in the absence of the embryo. HANSTEEN (12) and PURIEWITSCH (17), however, maintained that the endosperm is capable of self-depletion provided the hydrolytic products are removed. The later work of Miss BRUSCHI (6) harmonizes these divergent views by showing that while self-digestion can occur in various kinds of grains, it does so to such different degrees that earlier investigators, working each upon a single form only, reached contradictory conclusions.

Of more direct bearing upon the subject is the work of LECLERC and BREAZEALE (14), in which by macrochemical analyses a quantitative study was made of the effects of different culture media upon the amounts of various organic and inorganic substances found in the several portions of the wheat seedling at different stages of germination. One of the latest contributions to the question of chemical changes during germination is that of Miss ECKERSON (11), who finds that in light-sensitive seeds active hydrolysis of hemicelluloses, fats, and proteins in the endosperm occurs in both light and darkness, but that in the light this process

begins toward the outside of the endosperm, the resulting substances diffusing out and away from the embryo, while in the dark it begins near the embryo, which can then make use of the hydrolytic products. The presence of iron in the seed coat, acting catalytically in the light, is undoubtedly a factor in the first case.

With the development of microchemical technique a method has become available by which qualitative determinations can be made for the presence or absence of many substances without an undue expenditure of time, and in this way, especially when checked with macrochemical analyses at crucial points, the time and place of chemical changes can be determined with greater accuracy than heretofore, as the following results show.

Method

The material used in this study was Marquis wheat, a hard spring wheat, procured from the Albert Dickinson Company of Chicago in the fall of 1917 and again in 1919. In most cases the ungerminated grains were soaked for two hours in distilled water in order to facilitate sectioning. No differences could be observed in the chemical condition of grains thus soaked as compared with unsoaked ones. For germinated material the grains were soaked for two hours and then placed in covered Petri dishes with moist filter paper on the bottom. These dishes were placed in a dark room kept at 16°–20° C., unless otherwise noted. When the period of germination covered several days the dishes were opened daily and the air renewed. Sections were cut freehand, and the microchemical tests employed were those recommended in the standard works by MOLISCH, TUNNMANN, and CHAMOT. A list of the tests used will be found at the end of this paper. Methods used in determinations other than microchemical ones are described in appropriate places. The germination period was regarded as seven days, in part because of the difficulty of growing seedlings longer under the given conditions, but mainly because by the end of that time the seedlings had so far developed that, had they been growing under field conditions, they would have been making their own food, without dependence upon the endosperm.

Microchemical study

UNGERMINATED GRAIN

COAT.—As the coat of the grain is easily permeable and in no way delays germination, no particular study was made of it. In general it consists of four layers: (1) the outer portion of the pericarp, consisting of one or more layers of cells whose walls contain some pectic substance, (2) the inner epidermis of the pericarp, in which lignification has occurred, (3) the testa, also lignified, and (4) the suberized remnant of the nucellar tissue. Glucose is present in the pericarp, undoubtedly a remnant of that originally present in the pericarp of the developing fruit (ECKERSON 10).

ENDOSPERM.—*Carbohydrates.*—Large amounts of starch are found in the endosperm, except in the aleurone layer, where it is entirely lacking. No reducing sugars are present, but a small amount of sucrose can be identified.

Fats.—Most of the cells of the endosperm contain very little fat, but it is abundant in the aleurone cells.

Proteins.—Proteins also are found in the starch-containing cells of the endosperm, and these are known to be almost entirely the storage proteins, glutenin and gliadin (OSBORNE 16). These cannot be distinguished from each other by microchemical methods. In the aleurone cells storage proteins are absent, but other protein material is present in considerable quantity.

Oxidizing enzymes.—No oxidase is found, but both peroxidase and catalase are present.

Minerals.—Little potassium is present, but considerable calcium and magnesium. Small amounts of phosphates were detected, while the aleurone layer has much iron. As noted under the embryo, no sulphur could be identified.

EMBRYO.—*Carbohydrates.*—Sucrose is the only storage carbohydrate found in the embryo of the Marquis wheat. In some forms, such as Emmer, starch is found in the scutellum.

Fats.—Fats are found in all parts of the embryo.

Protein.—The embryo gives a strong protein reaction, although probably no storage proteins are present. No amino acids can be detected by microchemical methods.

Oxidizing enzymes.—As in the endosperm, oxidase is lacking, but peroxidase and catalase are present.

Minerals.—Potassium and magnesium are present in considerable quantities. Calcium and phosphates could not definitely be identified, although undoubtedly present. Iron is found in abundance in the cells just under the epithelial layer. Sulphur could not be detected by any known microchemical methods.

Germinating grain

Carbohydrates.—No change is apparent in the contents of the grain (aside from the swelling due to absorption of water and softening of the tissues) until 10–12 hours after the material has been put into germinating dishes. At this time dextrin appears in the scutellum and coleorhiza, and starch in the root cap. At about the same time dextrin appears in the coleoptile and shortly afterward in the plumule. After 12 hours reducing sugar is found in the coleorhiza and appears also in the root, endosperm, coleoptile, plumule, and scutellum by the end of 24, 36, 48, and 96 hours respectively. After the appearance of the sugar in the coleorhiza and coleoptile, the amount of dextrin present decreases and the amount of sugar increases. In the root the amount of sugar increases up to the fourth day, after which the sugar content does not increase proportionately with the increase in the root tissue. At all times it is found most abundantly in the zone of the root hairs. In the endosperm reducing sugar is first found near the basal end of the embryo, but eventually is found throughout the whole tissue. All tests indicate that this reducing sugar is glucose. At the end of seven days starch is still present in the greatly disorganized endosperm, although practically all the grains still remaining show marked corrosion. A summary of this microchemical study will be found in table I.

The following quantitative study of the sugars in germinating wheat made by LeClerc and Breazeale (14) is of interest in checking up these microchemical findings. As the seedlings studied by these investigators were apparently grown in the light, photosynthesis may have influenced the result, although within the period of only seven days this would hardly be an appreciable

TABLE I

SUMMARY OF MICROCHEMICAL ANALYSES FOR DETERMINING PRESENCE OF STARCH AND REDUCING SUGARS IN GERMINATING WHEAT (16°–20°C.); +, PRESENT; ++, PRESENT IN ABUNDANCE.

HOURS IN GERMINATOR	LENGTH OF COLEOPTILE (MM.)	ENDOSPERM		SCUTELLUM		COLEORHIZA		ROOT CAP		ROOT TIP		ROOT		COLEOPTILE		PLUMULE	
		Starch	Reducing sugar	Starch	Reducing sugar	Starch	Reducing sugar	Starch	Reducing sugar	Starch	Reducing sugar	Starch	Reducing sugar	Starch	Reducing sugar	Starch	Reducing sugar
6.....	0*	++	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10.....	0	++	0	+†	0	+†	0	+	0	0	0	0	0	0	0	0	0
12.....	0	++	0	+	0	+†	0	+	0	0	0	0	0	+†	0	0	0
18.....	0	++	0	+	0	+†	+	+	0	0	0	0	0	+†	0	+†	0
24.....	0	++	+	+	0	+†	+	+	0	0	0	0	+	+†	0	+†	0
36.....	0	++	+	+	0	+†	+	+	0	0	0	0	+	+†	0	+†	0
48.....	2.7	++	+	+	0	+†	+	+	0	0	0	0	++	+†	+	+†	+
72.....	3.1	++	+	+	0	0	+	+	0	0	0	0	++	+†	++	0	+
96.....	6.6	++	+	+	+	0	+	+	0	0	0	0	++	+†	++	0	+
120.....	16.8	+	+	+	+	0	+	+	0	0	0	0	++	+†	++	0	+
144.....	32	+	+	+	+	0	+	+	0	0	0	0	++	+†	++	0	+
168.....	49	+	+	+	+	0	+	+	0	0	0	0	++	+†	++	0	+

* Plumule not well through coat until 36 hours.

† Dextrin.

factor. No statement is made in regard to the variety of wheat used. Table II is the summary of results, as given by LECLERC and BREAZEALE.

TABLE II

Part of plant and age	Reducing sugar as dextrose (mg.)	Hydrolyzable sugar as dextrose (mg.)
For 100 seeds		
Original seed	0	96
Seeds		
3 days	98.6	60
5 days	192.4	53
7 days	193.8	60
Axes		
3 days	148.0	50
5 days	253.7	42
7 days	267.9	46
Total plants		
3 days	246.6	110
5 days	446.1	95
7 days	461.7	106

Proteins.—Although both embryo and endosperm in the ungerminated grain give protein reaction, the storage proteins are known to exist only in the endosperm. During germination these are broken down, and at the end of seven days the nearly exhausted remnant of the endosperm gives only a very slight protein reaction. At this time, however, the aleurone layer is still intact, apparently unchanged.

No satisfactory microchemical tests are known for the derived proteins such as proteoses and peptones, so that no determination could be made for these substances. Some of the amino acids can be crystallized out of the tissue and the crystals identified by their chemical and optical properties. The first amino compound to be identified is asparagine, which was observed in the coleoptile on the fourth day and slightly later in the root. After the first appearance of asparagine in the coleoptile it accumulates there rapidly. A further discussion of the amino compounds in the seedling will be found in a later paragraph. At all times a marked protein reaction is obtainable in the stem and root tip, especially the latter (text fig. 1).

Oxidizing enzymes.—At no time was oxidase found in any part of the germinating seedling, but peroxidase and catalase were

present in all parts. In view of the increasing interest in the question of catalase activity, quantitative determinations were made on the seedlings on each successive day of the germination period. The method employed was that of APPLEMAN (**1, 2**) as used by JONES (**13**). In each instance three sets of 5 grains each were used. The air-dry weight of each set was determined; one set was then used for determining the final dry weight, and duplicate determinations were made on the other two, the results of which are given in table III. This shows that there is a marked and continuous increase in the catalytic activity of the seedlings during the first seven days of germination. Within the past few years investigations upon both plants and animals have shown a striking relation between the rate of catalytic activity and that of respiration. BURGE (**7**) showed a marked correspondence between the amount of catalase in different muscles of the body and the amount of work done by these muscles, and APPLEMAN (**1, 2**) has shown a direct increase in the catalase content in potatoes and corn with an increase in the respiration. RISCHAVI'S (**18**) standard work has given excellent data on the respiration of wheat as indicated by the release of CO_2 during a period of 21 days. Text fig. 2 shows the comparative curves of the rate of respiration as plotted from RISCHAVI'S figures for the first seven days, and that of catalytic activity during a similar period from the figures obtained as given in table III. As in the investigations cited, there is here a close parallel between respiratory activity and catalytic activity.

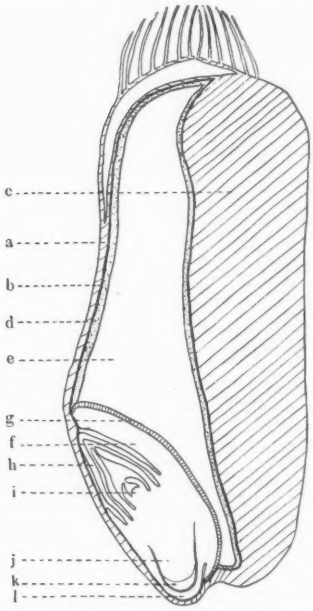

FIG. 1.—Longitudinal section of grain of wheat: *a*, pericarp and testa; *b*, suberized nucellar tissue; *c*, furrow in grain; *d*, aleurone layer; *e*, starchy endosperm; *f*, scutellum; *g*, epitheilal layer; *h*, coleoptile; *i*, plumule; *j*, hypocotyl; *k*, root cap; *l*, coleorhiza.

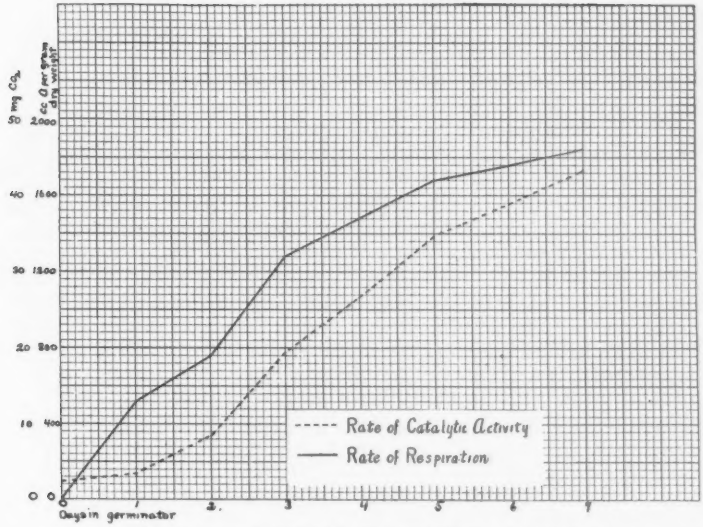

FIG. 2.—Relative rates of catalytic and respiratory activity (latter from RISCHAVI's data).

TABLE III

CATALASE ACTIVITY OF GERMINATING WHEAT

Days in germinator	Original dry weight (gm.)	Final dry weight (gm.)	Oxygen (cc.) released in 10 min.	Oxygen (cc.) released per gm. of dry weight (calculated)	Average
0	0.146	0.12848	10	78	84.5
	0.1496	0.1316	12	91	
1	0.1406	0.1251	14.6	116	132.5
	0.1401	0.12468	18.6	149	
2	0.1482	0.12967	42.2	325	334
	0.1331	0.11646	40	343	
3	0.143	0.1222	93.4	764	772
	0.1446	0.1236	93.6	781	
4	0.1485	0.1179	122	1034	1073
	0.1438	0.1141	127	1113	
5	0.1286	0.10288	126	1224	1379
	0.120	0.0768	119.6	1570	
6*					
7	0.1582	0.11849	198.4	1674	1726.5
	0.134	0.10036	178.6	1779	

* Complete data lacking.

Increase in length of epithelial cells.—During germination there is a marked increase in length in the epithelial cells of the scutellum. In wheat this increase amounts at the end of seven days to 119 per cent in the distal cells, that is, those near the brush end of the grain; 161 per cent in the intermediate cells; and 165 per cent in the basal cells. The actual amount of increase in size is given in table IV.

TABLE IV

INCREASE IN LENGTH OF EPITHELIAL CELLS DURING GERMINATION

HOURS IN GERMINATOR	LENGTH OF EPITHELIAL CELLS IN MM.		
	Distal	Intermediate	Basal
0	0.0347	0.0346	0.0273
12	0.0388	0.0402	0.0305
18	0.0377	0.0377	0.0314
24	0.0407	0.0429	0.0340
48	0.0455	0.0568	0.0436
72	0.0573	0.0703	0.0518
96	0.0638	0.0821	0.0592
120	0.0629	0.0880	0.0562
144	0.0769	0.0899	0.0677
168	0.0762	0.0906	0.0725

From the physiological studies of BROWN and MORRIS (**5**) and such cytological work as that of TORREY (**22**), it was believed that these epithelial cells actually secreted the diastase used in the hydrolysis of the starchy endosperm, and that this increase in size accompanied an increasing secretion of diastase. Miss BRUSCHI (**6**), however, stated that while there is a marked increase in the size of the epithelial cells at this time, the hydrolysis of the starch is due, not to diastase secreted by them, but to that developed from a proenzyme existing within the amyliferous endosperm cells, and that it is the action of this enzyme which causes the self-depletion of the endosperm even in the absence of the scutellum, while the scutellum itself, when separated from the endosperm and grown under sterile conditions, produces no diastase.

Quantitative study of amino nitrogen content

The crystallization of amino acids from wheat by microchemical methods is difficult, probably because of the large amount of storage

protein present, and accordingly in order to obtain more exact knowledge on this point macrochemical analyses were made.

Miss ECKERSON (10) has shown that in ripening wheat asparagine, arginine, histidine, and leucine are present. As the formation of the proteins proceeds during desiccation, these amino acids disappear almost entirely, and only a trace of asparagine is left in the ripened grain. LEHMAN and OLTENWÄLDER (15) stated that unripened seeds frequently germinate more readily than wholly ripened ones because of the presence in the former of amino acids and active proteolytic enzymes, while in fully ripened seeds these enzymes which hydrolyze the storage proteins into more available forms are not always present in an active state. All investigations thus far indicate an increase in the amino acid content of seedlings during germination. Undoubtedly the most important work on this subject has been done by SCHULZE and his associates (19, 20) on the seedlings of *Lupinus luteus* and other leguminous plants, although in most cases on seedlings older than the wheat under consideration. In general he found that the first amino acids to appear are leucine, tyrosine, and the hexone bases, and concluded that the asparagine found somewhat later is a secondary product, formed from the mono-amino acids which serve as a storage substance to be used again in protein building. As the growth of the seedling advances, the asparagine content increases, while the amounts of the earlier formed acids decrease. The earlier theory of DETMER'S (9) that asparagine is a primary product of protein hydrolysis, and that its accumulation in seedlings grown in the dark is due to the absence of carbohydrates to unite with it to form new protein, seems improbable, as SCHULZE found almost as much in seedlings grown in the light as in the dark, and microchemical analysis clearly shows large quantities of sugar present in the coleoptile together with the asparagine in the seedlings over four days old.

The object of the analysis recorded in table V was not to isolate individual amino acids, but simply to determine the total amount of such substances. Determinations were made at three stages: (*A*) the ungerminated grain, (*B*) seedlings 3.5 days old, and (*C*) seedlings 6 days old. The temperature of the

dark room in which these seedlings were grown was 21°–23° C., which probably accounts for the greater length of coleoptile and root as compared with seedlings of the same age used in studying the carbohydrates. In sample *A* the air-dry wheat was finely ground in a food chopper, and in *B* and *C* the seedlings were cut up into small pieces with scissors immediately after removal from the germinating dishes. In all cases the material was preserved in 70 per cent alcohol. After extraction in hot alcohol

TABLE V

ANALYSIS OF MARQUIS WHEAT (1917) FOR AMINO NITROGEN CONTENT

Sample	Percentage	Percentage dry weight	Percentage soluble nitrogen
A (ungerminated)			
Moisture	10.78		
Soluble nitrogen		0.164	
Amino nitrogen		0.0275	16.76
	Length of coleoptile 50 mm.		
B (germinated 3.5 days)			
Moisture	68.71		
Soluble nitrogen		0.837	
Amino nitrogen		0.29	35.53
	Length of coleoptile 90 mm.		
C (germinated 6 days)			
Moisture	82.83		
Soluble nitrogen		1.66	
Amino nitrogen		0.63	37.79

for six hours the material was ground in a mortar and a hot water extract made. As the presence of so much colloidal material (starch and protein) made it impossible to separate at all accurately the water from the solid matter, the entire mass was made up to 75 per cent alcohol, and all colloidal material precipitated by shaking with NaCl. The material was then filtered and the filtrate combined with the alcohol extracts and condensed in vacuo at 60°–70° C. to approximately 50 cc. This amount was then made up to volume (100 cc.) with distilled water. Determinations were made on this material for total nitrogen and

amino nitrogen. The former determinations were made by the BOCK and BENEDICT modification of the FOLIN-FARMER procedure (3), and this nitrogen is regarded as "soluble nitrogen" in table V. Determinations were made for amino nitrogen by the VAN SLYKE method. The results of these determinations are given in table V, from which it is seen that there is a considerable amount of amino nitrogen in the ungerminated grain, and that during germination this amount increases rapidly, while the increase in soluble nitrogen is less rapid. In comparison with these results, those obtained by THOMPSON (21) on the Alaska pea seedling are of interest. They are as follows:

PEAS	PERCENTAGE OF DRY MATERIAL	
	Total N	Amino N
Dry	....	0.088
3 days old	3.28	0.337
6 days old	3.48	0.747

It is also evident from the results given in table V that microchemical methods for identifying amino acids are not very satisfactory in the case of germinating wheat, probably for several reasons. The amino acids may be present in such small amounts that, although totaling an appreciable quantity, they cannot be detected individually; they may be those for which no satisfactory microchemical test has yet been found; or, as suggested earlier, other material present may prevent normal reactions from occurring. In the case of wheat such substances as storage proteins might easily interfere with the crystallization of the amino acids and so prevent their identification.

Summary

1. The principal storage carbohydrate of Marquis wheat is starch in the endosperm. A small amount of sucrose is also present in the endosperm and embryo.

2. The first noticeable chemical change during germination is the appearance in the scutellum and coleorhiza of dextrin, and in the root cap of starch. These substances appear simultaneously after about ten hours in the germinator (16°–20° C.). Later dextrin appears in the coleoptile and plumule.

3. Reducing sugar (probably all glucose) appears in the embryo after 18 hours in the germinator. It is first found in the coleorhiza, but soon afterwards appears in considerable quantity in all parts of the seedling, especially in the zone of root hairs and coleoptile.

4. During the germination period studied the increase in length of epithelial cells averaged 150 per cent.

5. Peroxidase and catalase are present in all parts of the grain both before and during germination. The amount of catalase present increases during the first seven days at a rate corresponding to the rate of increase in the respiratory activity.

6. During germination the protein content of the endosperm, except for that of the aleurone layer, decreases greatly.

7. Microchemical analyses show the presence of amino acids in the ungerminated grain and their increase in amount during germination. Microchemical analyses fail to indicate any amino nitrogen until the fourth day of germination. Asparagine is the only form that can then be so identified. This appears only in the root and coleoptile, accumulating in the latter in considerable quantity.

Microchemical tests

Pectic substances.—Ruthenium red, red color; methylene blue, violet color.

Lignin.—Phloroglucin and HCl, violet red color obtained without heating.

Suberin.—Insoluble in cold 50 per cent chromic acid.

Starch.—Iodine-potassium iodide, blue color.

Dextrin.—Amylo-dextrin, iodine-potassium iodide, red color; dextrin, precipitation of cuprous oxide upon long heating with Flückiger's reagent (see under fructose).

Fructose.—Flückiger's reaction; copper tartrate dissolved in 15–20 per cent NaOH, red precipitate obtained at once without heating.

Glucose.—Flückiger's reaction; red precipitate of cuprous oxide on heating 1–2 minutes; osazone crystals with phenyl-hydrazine reaction.

Sucrose.—First remove any fructose or glucose present as follows: apply Flückiger's reagent and, to remove any precipitate formed after heating for 2–3 minutes, wash with dilute tartaric acid solution, add warm concentrated magnesium chloride, and wash again in tartaric acid; then invert with invertase or dilute acid and test again with Flückiger's reagent.

Proteins (general).—Biuret reaction; xanthoproteic reaction.

Storage proteins.—Add $AlSO_4$ to form aluminium proteinate and then stain with logwood solution; not a specific reaction for individual proteins.

Amino acids and amides.—General test: Crystallize out in absolute alcohol; crystals of asparagine, glutamine, tyrosine, leucine, proline, and potassium nitrate may appear.

Specific tests: comparison with known crystal forms; observation with polarized light: asparagine, place sections in copper acetate, add absolute alcohol slowly and crystals of copper asparaginate appear; leucine, sublimation; arginine and histidine, picrolonic acid gives yellow crystalline precipitate.

Oxidizing enzymes.—Oxidase, blue color upon addition of guiaconic acid; peroxidase, blue color with guiaconic acid and H_2O_2; catalase, evolution of gas with addition of H_2O_2.

Minerals.—Calcium, with H_2SO_4 have calcium sulphate crystals; magnesium, formation of ammonium magnesium phosphate crystals; potassium, crystals of potassium-platinum-chloride upon addition of platinum chloride; iron, Berlin blue reaction (potassium ferrocyanide and HCl); phosphates, upon addition of magnesium mixture formation of ammonium magnesium phosphate crystals, upon addition of ammonium molybdate in nitric acid formation of ammonium phospho-molybdate crystals; sulphates, formation of benzidine sulphate crystals on addition of benzidine chloride.

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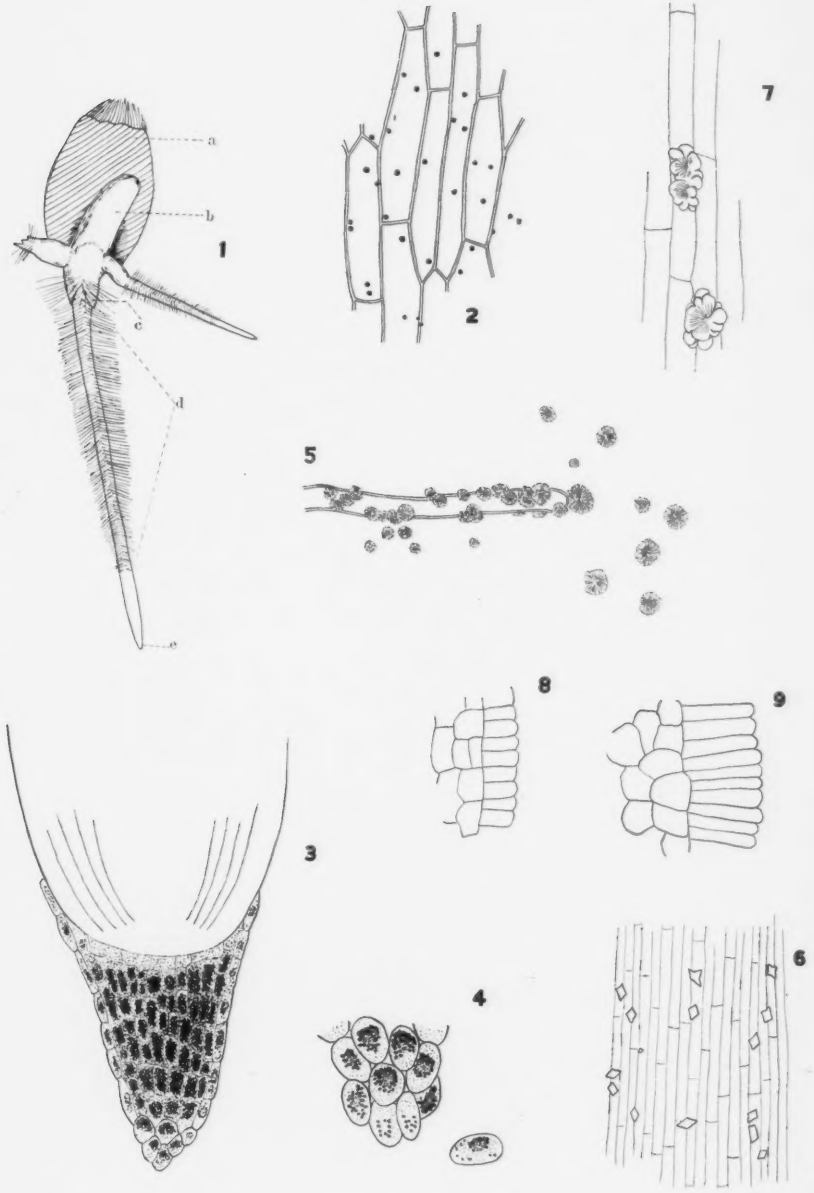

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EXPLANATION OF PLATE XXVIII

FIG. 1.—Wheat seedling, two days old: *a*, old kernel; *b*, coleoptile; *c*, coleorhiza; *d*, zone of root hairs; *e*, root cap; ×4.5.

FIG. 2.—Outer layer of pericarp showing cuprous oxide precipitated by Flückiger's reagent; ×150.

FIG. 3.—Root cap, showing starch stained with iodine (3 days old); ×112.

FIG. 4.—Detail of root cap; ×175.

FIG. 5.—Root hair showing crystals formed by osazone test; ×275.

FIG. 6.—Asparagine crystallized out in absolute alcohol in coleoptile (material 7 days old); ×45.

FIG. 7.—Copper asparaginate formed by addition of copper acetate and absolute alcohol in coleoptile (material 7 days old); ×150.

FIG. 8.—Epithelial cells of scutellum when placed in germinator; ×150.

FIG. 9.—Epithelial cells of scutellum after 7 days in germinator; ×150.

UNDESCRIBED WILLOWS OF THE SECTION CORDATAE

CARLETON R. BALL

(WITH ONE FIGURE)

While this paper is a continuation of the series which has appeared under the title *Notes on North American willows*,[1] this general title is dropped now in favor of a specific one for each contribution. This seems desirable because it will permit a clear indication of the contents of each paper in the title thereof. These papers have resulted chiefly from studies made in preparing the treatment of the genus *Salix* for different floras and manuals of botany.[2]

The location of the herbarium material cited is indicated by capital letters in parentheses, as follows: B, herbarium C. R. Ball; C, herbarium Canadian Geological Survey, Ottawa; F, Field Museum, Chicago; FBb, Bebb Herbarium of Field Museum; Fs, Forest Service, United States Department of Agriculture; G, Gray Herbarium, Harvard University; I, Iowa Agricultural College; N, United States National Herbarium; R, Rocky Mountain Herbarium, University of Wyoming; RMP, herbarium of Rocky Mountains Park, Banff, Alberta, Canada.

SALIX LUTEA **famelica,** n.var.—Shrub or small tree, 3–6 m. tall; branchlets grayish, those of the season yellow, rather short and divaricate, glabrous: leaves small, stipulate; stipules mostly minute, 1–3 mm. long, ovate to lanceolate, acute; petioles slender, 4–8 mm. long, yellowish, glabrous; blades linear-oblanceolate, narrowed and acutish or somewhat rounded at base, acute to

[1] BOT. GAZ. **40**:376–380. *pls. 12, 13.* 1905; **60**:45–54. *figs. 1–3.* 1915; **60**:391–399. 1915.

[2] BALL, CARLETON R., *Salix* in COULTER and NELSON, Man. Bot. Rocky Mountain Region. pp. 128–139. 1909.

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———, *Salix* in CHAS. C. DEAM, Trees of Indiana, revised ed. pp. 34–45. *pls. 10–14.* 1921.

acuminate at apex, 5–6 cm. long, 8–10 mm. wide, on vigorous shoots 7–10 cm. long, 12–20 mm. wide, yellowish green, glaucous beneath, glabrous and strongly reticulate on both sides, margins cartilaginous and shallowly serrulate, or subentire: pistillate aments small, 2–3 cm. long, on short peduncles 1–3 mm. long, subtended by 2 or 3 small leaves: capsule glabrous, lanceolate, 4.5–5 mm. long; pedicel 1–1.8 mm. long.

This variety differs from *S. lutea* chiefly in the very small and more strongly nerved leaves. The aments and the pedicels both are shorter than the average for the species. It holds much the same relation to *S. lutea* as var. *angustata* does to *S. cordata*. The demarcation seems sharper in the present case, but this may be due to the limited number of specimens in hand. The name means starved or hungry, and is suggested by the attenuate leaves with their prominent "ribs."

The earliest collection seen by the writer was made in 1883 by *L. F. Ward*, on an island in the Yellowstone River, 12 miles above Glendive, Montana. The type was collected by the writer about 120 miles farther up the Yellowstone River. *S. lutea* is very abundant on the floodplain of the river at Forsyth, Montana. Several clumps of shrubs were examined, probably fifteen or twenty in all, but only one was referable to the present variety. It consisted of only two or three stems, 8–10 cm. in diameter at the base, and 5–6 m. tall, located scarcely more than 10 rods from the north edge of the little town. It was recognized at sight as differing in some way from the other clumps, and this difference was found to be in the size of the leaves.

WARD'S specimen almost exactly matches the type, although the leaves are younger and smaller, the date of collection being six weeks earlier. The specimen from the Bellefourche River in South Dakota resembles *S. cordata angustata* a little more, just as the specimens of *S. lutea* from the Black Hills vary somewhat toward *S. cordata*. Further search probably will locate the variety in other parts of the Yellowstone Valley and in other districts. The first four specimens cited are all from one general district. The Bitter Root specimen is fragmentary and not well preserved, and hence somewhat doubtfully referred here.

SOUTH DAKOTA.—Bellefourche, along Bellefourche River, *C. R. Ball* 1347, September 19, 1908 (B).

NORTH DAKOTA.—Marmarth, wet bottoms, Little Missouri River, *L. C. Moyer* 469, June 6, 1914 (B).

MONTANA.—Osprey Island in Yellowstone River, 12 miles above Glendive, *L. F. Ward*, July 17, 1883 (FBb 2380); Forsyth, north edge of town, *C. R. Ball* 1304, September 1, 1908 (B, type; N); Bitter Root Valley and Mountains, Warm Springs Creek, alt. 7500 ft., *Pammel* and *Fawcett*, August 21–September 2, 1904 (B, I).

SALIX LUTEA **ligulifolia,** n. var.—*S. cordata*, in part, as interpreted by BEBB, *Willows of California*, 85, 1879, and BEBB in COULTER, Man. Bot. Rocky Mt. Reg. p. 335. 1885.—*S. cordata Watsoni*, in part, as interpreted by BALL, in COULTER and NELSON, New Man. Rocky Mt. Bot. p. 132. 1909.

When first studied this willow was regarded as a species intermediate between *S. cordata* and *S. lutea*, and a detailed description was written. Later it was considered more properly placed as a variety of *S. lutea*, but the complete description has been allowed to stand. It is hoped that fuller field study may be given to this interesting form.

Shrub with clustered stems 1.5–3.5 m. tall; bark dark gray; branchlets elongated, dark brown or somewhat yellowish, glabrous and usually shining, or the youngest pubescent; buds ovate-lanceolate, 5–10 mm. long, acute or obtusish, glabrous or pubescent, bright chestnut to dark brown, drying black: leaves mid-sized, petiolate, stipulate; stipules semicordate and acute to semilunate and obtuse, 4–10 or more mm. long, entire or serrulate, glabrous, glaucous beneath; petioles 6–10 mm. long, dark brown, glabrous to puberulent to pubescent, as the twigs; blades ligulate-lanceolate or oblong-lanceolate (narrowly oblanceolate when young), acute or very short-acuminate, rounded or subcordate and usually oblique at base, 5–10 cm. long, 1–2 cm. wide, common sizes 5 by 1.2–1.5, 7 by 1.3–1.8, 8 by 2, 9 by 1.5–2, and 10 by 2, cm., entire or (especially on vigorous sterile shoots) shallowly and remotely serrulate or glandular-serrulate, reticulate on both sides, especially beneath, dark green above, pale and at maturity usually white glaucous beneath, glabrous throughout or the white midrib puberulent above near base: aments appearing with the leaves or somewhat precocious, sessile, or the pistillate on peduncles 3–5 mm. long; pistillate aments 2–3.5 cm. long, subsessile, or on peduncles 3–5 mm. long, subtended by 2–4 very small leaves; scales elliptic-oblong, obtusish, drying black, glabrate outside at apex, basal portion and inside densely white-tomentose: capsule small, lanceolate or ovate-lanceolate, 4–5.5 mm. long, glabrous; pedicel 1–1.5 mm. long, glabrous; style 0.3–0.5 mm. long; stigmas short, entire, notched or bifid: staminate aments sessile, naked at base, or with one or two small bracts, slender, 2–3 cm. long, 4–8 mm. wide;

stamens 2, filaments slender, glabrous, free; scales as in pistillate ament.

S. lutea ligulifolia is a mountain-loving form. It is found in the Rocky Mountain system from the Black Hills of South Dakota, and the Laramie Hills and Medicine Bow Mountains of southeastern Wyoming, south to southern New Mexico and central Arizona. An isolated distribution occurs in extreme western Nevada and the adjacent Yosemite Valley of California. It appears to be confined to stream banks in mountain canyons at elevations from 5000 ft. (1500 m.) to probably 9000 ft. (2700 m.), although its upper limits are unknown as yet. It flowers from the last week in April until well into May, and fruits in due season thereafter.

It is distinguished from typical *S. lutea* by usually dark brown branchlets, longer and narrower, straplike, usually dark green leaves, with the margins often nearly parallel and usually entire or only shallowly serrulate. The capsules also are shorter and on fairly short pedicels. Specimens collected when the leaves are just unfolding resemble *S. irrorata*, but may be distinguished by somewhat lighter colored twigs, without the glaucous bloom, and by the broader, less oblanceolate leaves and longer pedicels. The following specimens are referred here.

CALIFORNIA.—Yosemite Valley, *H. N. Bolander* 6331, June 3, 1866 (FBb 6335, N).

NEVADA.—Washoe County, Hunter's Canyon, vicinity of Reno, 1350–1500 m., *A. E. Hitchcock* 455, July 18, 1913 (N); no locality (probably Washoe County) *Lieut. Wheeler*, 1872 (N, twig densely pubescent); Soda Springs Canyon, Mineral (Esmeralda) County, *W. H. Shockley* 363, May 1886 (FBb).

ARIZONA.—Grand Canyon, Indian Gardens, alt. 3800 ft., *E. A. Goldman* 2237, August 25, 1913 (N, twig densely pubescent); Navajo County, Black Mesa Forest Reserve: Black Canyon, Houck's Ranch, *F. V. Coville* 1084, June 5, 1900; along creek at Showlow, *Coville* 1091, June 8, 1900; 2022, July 4, 1904 (N, both specimens with pubescent-pilose young twigs and broader and more serrulate leaves); Apache County, Springerville, alt. 7000 ft., *E. A. Goldman* 2446, June 8, 1915 (N); White Mountain Indian Reservation; watershed of White River above Ft. Apache, *Coville* 1977 (N 500639, type), 1981, June 30, 1904 (N); White Mountains, south of Thomas Peak, *Coville* 2014, July 2, 1904 (N); along White River near Ft. Apache, *Coville* 2016 and 2020 (seasonal twigs pubescent, leaves broader and more serrulate), July 3, 1904 (N); White Mountains, head of Black River, *L. N. Goodding* 1212, July 18, 1912 (N); White Mountain Apache Reservation, *Myrtle Zuck*, June 25, 1907 (N).

UTAH.—Kane County, Three Lakes, north of Kanab, *I. Tidestrom* 2417, July 9, 1909 (B).

NEW MEXICO.—No locality (probably Silver City, Grant County), *E. L. Greene* (FBb 3908, in part); Grant County, Ft. Bayard, Stephen's

Ranch, *J. C. Blumer* 171, November 15, 1905 (B); Lincoln County, White Mountains, alt. 7000 ft., *E. O. Wooton* 307, August 10, 1897 (N); Union County, Cross L. Ranch, head of Cimarron Canyon, *D. Griffiths* 4305, May 11, 1903 (B, N).

COLORADO.—Montezuma County, Mancos, *Alice Eastwood* 22, June 1891 (N); La Plata County, Durango, *Alice Eastwood* 23, June 1891 (N); Saguache County, Cochetopa National Forest, near Big Meadows, alt. 9500 ft., *W. O. Sanders*, July 8, 1916 (B); Conejos County, Los Pinos, alt. 7000 ft., *C. F. Baker* 270 (in part), May 1899 (F, N); Las Animas County, Stonewall, *Johnston* and *Hedgcock* 498, June 18, 1917 (B); Costilla County, Blanca, alt. 7752 ft., *E. R. Warren* 72; July 16, 1912 (B); Pikes Peak district, Little Fountain Creek, *J. C. Blumer* 5, 6, September 5, 1903 (B); Manitou, alt. 6000 ft., *M. E. Jones* 30, May 8, 1878 (N, twigs pubescent); Park County, Cassells, *E. W. Cathcart*, June 1904 (N); Lat. 39°–41°, *Hall* and *Harbour* 524, 1862 (FBb); Routt County, Walcott, *Alice Eastwood* 17 (in part), July 1891 (FBb).

SOUTH DAKOTA.—Custer County (Black Hills), Beaver Creek, Mayo, *W. H. Over* 1857, June 18, 1914 (N).

WYOMING.—Albany County, Little Laramie River, *L. N. Goodding* 5, 6, June 14, 1901 (B); foothills west of Islay, alt. 7300 ft., *Merritt Cary* 313a, June 25, 1909 (N).

SALIX LUTEA **platyphylla,** n. var.—*S. cordata* var. Bebb in KING, U.S. Geol. Explor. 40th Parallel **5**:325. 1871.—Shrub or small tree 3–6 m. tall; branchlets virgate or somewhat divaricate, yellow, shining, glabrous; buds yellow: stipules mostly small, semicordate to sublunate; petioles very slender, 8–15 mm. long, yellow, glabrous; blades differing from those of the species in being broader and shorter, elliptic-obovate, acute or short-acuminate at apex, broad and rounded or obliquely subcordate to cordate at base, 1.5–3 cm. wide, 4–8 cm. long, common sizes being 2 by 4, 2–2.5 by 5, 2–2.5 by 6, and 2.5 by 7 cm., while sprout leaves reach such dimensions as 3.5 by 8, 4.5 by 9, and 4–4.5 by 11 cm.: aments same as in the species except that capsules are longer stalked, pedicels ranging from 1 to 2.5 or sometimes 3 mm. in length.

This variety occurs rather commonly in the Wasatch Mountain system from southwestern Utah to Idaho and ranges thence northwestward into Oregon. It is probable that it is more abundant than the specimens cited would indicate. It is separated from *S. lutea* by the broad, ovate-lanceolate leaves and the more elongated pedicels, 1.5–2.5 or 3 mm. long. In flowering specimens, however, neither the broad leaves nor the elongated pedicels are certainly distinguishable. It is almost exactly the form described by BEBB as "*S. cordata* var." NUTTALL describes *S. lutea* as having ovate-lanceolate

leaves, but states that they are more lanceolate than ovate. This statement agrees with NUTTALL's figure (Sylva 1:63. *pl. 19*) and with the form of leaf on the cotype specimen, in which the pedicels are very short, scarcely exceeding 1 mm. The following specimens are referred to this variety.

UTAH.—Beaver County, Milford, *L. N. Goodding* 1020, June 4, 1902 (B, N); Juab County, Nephi, *C. R. Ball* 94, October 8, 1907 (B, N) and (by *F. D. Farrell* from same plant) June 19, 1909 (B); San Pete County, common in Coal Canyon, San Pitch Mountains, *I. Tidestrom* 1304, June 24, 1908 (N); Carbon County, Indianola, *I. Tidestrom* 2247, June 17, 1909 (B); Salt Lake City, City Creek Canyon, alt. about 6000 ft., *M. E. Jones* 1702, May 11, 1880 (N); alt. 5000 ft., *S. G. Stokes*, May 1, 1900 (N); *P. A. Rydberg* 6040, June 9, 1905 (N); *C. R. Ball* 1335, 1336 (B, type) September 11, 1908 (B, N); Farmington Canyon, near Salt Lake City, *Pammel* and *Blackwood* 3618, July 14, 1902 (B, I); Peterson, Weber River, alt. 6500 ft., *Pammel* and *Blackwood* 3903, July 18–24, 1902 (B, I); Ogden Canyon, Ogden, *A. E. Hitchcock* 1481, August 19, 1913 (N); Ogden, alt. 4300 ft., *M. E. Jones* 6552, May 29, 1889 (N).

WYOMING.—Sweetwater County, Bush Ranch, *A. Nelson* 7103, June 10, 1900 (B).

IDAHO.—Bear Lake County, Montpelier, *J. F. McBride* 17, May 15, 1910 (G, N with specimen of *S. caudata*); Canyon County, along the river, Emmett, alt. 2200 ft., *J. F. McBride* 790, April 29, 1911 (N).

OREGON.—Blue Mountains, head of Otis Creek, *W. C. Cusick* 1645, June 15, 1897 (N); Sherman County, Moro, *C. R. Ball* 1853, August 4, 1914 (B, N), *C. R. Ball* 2010, 2011, June 29, 1915 (B, C, F, G, I, N, R); Grass Valley, *C. R. Ball* 2012, June 30, 1915 (B); Des(c)hutes River, *Thos. Howell*, May 1886 (N).

NEVADA.—Humboldt County, Santa Rosa National Forest, mouth of Hansen Creek Canyon, alt. 4800 ft., *B. S. Martineau* 26 (in part), May 7, 1915 (B, Fs).

Salix monochroma, n. sp.—*S. cordata* in part, of various authors treating of the Pacific northwest, not of Muhl.—*S. pyrifolia* as interpreted by BALL, in COULTER and NELSON, New Man. Rocky Mt. Bot. p. 133. 1909, not of ANDERSSON, 1867, or of SCHLEICHER, 1815.—*S. rotundifolia* Nutt., N. A. Sylva 1:75. 1842, not TRAUTVETTER, 1832.—Low shrub, with slender, glabrous, shining branchlets and small stipules: leaves obovate-oval or ovate, short-acuminate, 4–8 cm. long, crenulate-serrulate, thin, deep green and glabrous on both sides: aments appearing with the leaves, pistillate short-pedicelled lax; scales lanceolate-oblong, acute, dark, thinly pilose; capsule lanceolate, acute, 5–6.5 mm. long, glabrous; pedicel 2–4 mm. long, style about 0.5 mm. long; staminate ament sessile, slender; stamens 2, filaments glabrous, more or less united.

FIG. 1.—*Salix monochroma* Ball: portion of *Coville* and *Kearney* 241, from Idaho; leaves typical but ament smaller than usual (about two-thirds natural size).

Low shrub, 1–3 m. high; bark gray; branchlets slender, mostly elongated and virgate, sometimes shorter and divaricate, yellowish or bright chestnut to brown, glabrous, shining, full of leaf scars; buds slender, 4–7 mm. long, acute, chestnut to dark brown, glabrous, inconspicuous: leaves stipulate, petiolate; stipules narrowly ovate to lunate, crenate-serrulate to denticulate, color and texture as in blades; petioles slender, 4–8 or 10 mm. long, or to 15 mm. long on sprout leaves, yellowish to dark brown, glabrous or puberulent; blades elliptic-oblanceolate to obovate-oval or ovate, acute to short-acuminate, or distal ones acuminate, 4–8 cm. long, 1.5–4 cm. wide, common sizes being 4 by 2, 5 by 2.5, 6 by 2.5–3.3, 7 by 2.5–3.5, 8 by 3, rounded to truncate or slightly cordate at base, glandular crenate-serrulate, those on luxuriant sterile branchlets and sprouts much larger, 8 by 4 or 10 by 3.5 cm., all thin, translucent, deep rich green on both sides, primary and secondary veins slender and somewhat raised on both surfaces, glabrous, at first thinly pilose-pubescent: aments slender, lax, appearing with the leaves, on short leafy peduncles; pistillate peduncle 5–8 or sometimes 13 mm. long, pubescent, bearing 2–4 small leaves 1–3 cm. long; staminate aments nearly sessile; pistillate ament 2.5–6 cm. long, 1.5–2 cm. wide, lax; capsule lanceolate or rostrate from a subovoid base, 5–7 mm. long, glabrous; pedicel slender, 2–4 mm. long; style 0.4–0.6 mm. long, stigmas short, stout, mostly notched; scales elliptical-oblong or oblanceolate, light brown, drying black, acute or obtusish, thinly clothed outside and more densely so inside with long crinkly hairs; gland 1, linear-clavate, elongated, sometimes 1.3 mm. long, usually shorter; staminate aments sessile, 2.5–6 cm. long (subtended by 2–3 leaves 1–2 cm. long), 1 cm. wide, slender, scales as in pistillate aments; stamens 2, filaments glabrous, united for 0.5–0.7 of their length.

S. monochroma ranges from the Yellowstone Park of northwestern Wyoming and adjacent Montana to the Willamette Valley of western Oregon and north to southern British Columbia and southern Alberta. It is a shrub of stream banks in the mountains of this section. Apparently it ranges in altitude from about sea level (Portland) to 5000 or 6000 ft. (1500 to 1800 m.) in the mountains, or occasionally to somewhat higher elevations. The flowers appear from about April 15 to May 15, and fruit follows in due season. At the higher altitudes the dates are considerably later. The writer was in error in placing

this species under the name *S. pyrifolia* in the *New Manual of Rocky Mountain Botany*. This was due to a misinterpretation of ANDERSSON'S species. This species is found quite commonly in at least four states and sparingly in others, and is represented by fairly abundant herbarium material. It seems never to have been described previously, however, unless NUTTALL'S *rotundifolia* is correctly interpreted as belonging here. *Nelson's* 6101 from the Yellowstone Park comes the nearest of any of the specimens cited to matching NUTTALL'S description.

S. monochroma is most closely related to *S. mackenziana* on the one hand, and to *S. pseudomyrsinites* on the other. From *S. mackenziana* it is separated by the very thin leaves, more ovate in outline and never even glaucescent, but colored deep green alike on both sides. From *S. pseudomyrsinites* it may be separated by the much thinner and broader leaves, less glandular, and with much more slender veins. The pedicels also are shorter and usually glabrous. The following specimens are referred to this species.

WYOMING.—Yellowstone National Park, *E. A. Mearns* 633, May 11, 1112, June 15, 1363, June 24, 1902 (N); in a ravine in the woods, Obsidian Creek, 2–4 ft. high, *Aven Nelson* 6101, July 24, 1899 (B).

MONTANA.—Livingston, *E. W. Scheuber*, June 1, 1901 (N).

IDAHO.—No locality (probably Boise or northward), *Coville* and *Kearney* 241 (N), 244, May 1899 (B, N); Cuddy Mountains, Washington County, alt. 6000 ft., *M. E. Jones* 6547, July 11, 1899 (N); Nez Perces County, valley of Hatwai Creek, *Sandberg*, *MacDougal*, and *Heller* 39, April 24 (G, N, 935072, type, female; 242995, type, male), 70, April 28 (N); valley of Clearwater River (on island) 96, May 2 (F, G, N); valley of Peter Creek, 117, May 4 (FBb 2679, G, N); canyons, valley of Lake Waha, 215, May 21 (FBb 2828, G, N); along Hatwai or Peter Creeks, 1046, May 4, or 10, 1892 (N, 2 sheets); about Lewiston, *A. A.* and *E. G. Heller* 2942, April 23, 1896 (N); Latah County: *L. F. Henderson* 2880 (Wessels), 7894 (FBb); along Paradise Creek, near Moscow, *Henderson* 2882 (in part), June 2, 1894 (FBb); along the Potlatch River, near Juliaetta, *Henderson* 2883, April 21, 1894 (FBb).

OREGON.—Blue Mountains, mostly Union County: common along streams, Union County, *Cusick* 875, 1880; alt. 8000 ft., *Cusick* 968 (in part), September 1882 (N); Crane Prairie, South Blue Mountains, *Cusick* 1652 (in part), June 17, 1897 (N); stream banks, *Cusick* 1845, April 26, May 9, September 1898 (N); bank of Catherine Creek, alt. 3500 ft., *Cusick* 2383, May 30, June 28, 1900 (F, G, N); Union, *G. R. Hyslop* 2058, July 18, 1916 (B); Wallowa County: along Chesnimnus Creek, Chico Station, Imnaha National Forest, alt. about 1000 m., *Coville* 2328, May 27, 1907 (N); Headwaters of Mud Creek, alt. about 1350 m., *Coville* 2390, June 8, 1907 (N); Umatilla County, ford of Umatilla River, South of Mission and 5 miles east of Pendleton, *C. R. Ball* 2089, August 20, 1917 (B); Grant County, Izee, *Griffiths* and *Hunter* 199, July 15, 1902 (B); Deschutes River, *Thomas Howell*, May 9, 1885 (FBb); Bend, on Deschutes River, *E. Nelson*, May 22, 1905 (B); Linn County, Fish

Lake, *F. A. Walpole* 305, August 1, 1899 (N); Portland, *L. F. Henderson*, 1886 (FBb 6234).

WASHINGTON.—Whitman County, Pullman, *A. D. E. Elmer* 111, May 1897 (B); *C. V. Piper* 3598, May 13, 1898 (B); Walla Walla County, Waitsburg, *R. M. Horner* 446, April 22 (N), 447, April 9, 1897 (N); (west) Klickitat County, Columbia River, *W. N. Suksdorf* 40, April 25, 1884 (B); no locality, probably Klickitat County, *E. P. Sheldon* 8124, 1897 (N); Kittitas County, Wenatchee Mountains, *Coville* 1177, September 4, 1901 (N); Okanogan County, along Ashnola River, Sheep Mountain—Bald Mountain Trail, Okanogan Forest, alt. 1630 m., *W. W. Eggleston* 13395, August 2, 1916 (N).

ALBERTA.—Rocky Mountain Park, vicinity of Banff, *N. B. Sanson* 119, June 9 and 20, 1911; 257, 260, 262, 263, 264, 266, 267, 299, 302, 311, between July 4 and July 15, 1911; 341, 380, 387, 2038, between August 2 and August 14, 1911; 511, June 29, 1912, ≡ July 1, 1912 (B, RMP).

SALIX FARRAE **Walpoleii** Coville and Ball, n. var.—Low shrub, 0.5–2.5 m. high; bark probably dark gray; branchlets substoutish, the older dark gray to brown, those of the season, or of two years' growth, mostly short, divaricate, dark brown to black, the youngest pubescent with gray hairs, becoming glabrate or glabrous, all rather closely beset with bud scars; buds (seen only on flowering and fruiting specimens) minute or small, 1–3 mm. long, lanceolate-conic, black, thinly pubescent or glabrous: leaves mid-sized, petiolate, minutely stipulate; stipules minute to small, lanceolate or semicordate to ovate, acute, entire or denticulate, 1–5 mm. long; petioles slender, 2–10 mm. long, yellowish to dark brown, pubescent, becoming glabrous; blades elliptic-lanceolate to obovate, acute or abruptly short-acuminate, 4–8 cm. long, 2–3.3 cm. wide, common sizes being 5 by 2–2.5, 6 by 2–2.5, 7 by 2.4–3, and 8 by 3.3 cm., narrowed to somewhat rounded at base, entire or shallowly and rather remotely crenulate, thin, glabrous, green above, glaucous beneath, coarsely reticulate with slender veins on both surfaces: aments slender, rather lax, appearing with the leaves, on leafy peduncles; pistillate peduncle 1–2 cm. long, bearing 2–4 leaves 2–4 cm. long; the staminate 5–10 mm. long, bearing 2–3 leaves 1.5–2.5 cm. long: pistillate aments 2–5 or 6 cm. long, 12–15 mm. wide, lax in fruit, rachis scantily tomentose; capsule narrowly lanceolate-rostrate, or conic-rostrate, 5–7 mm. long, mostly obtuse, brown, glabrous; pedicel slender to stoutish, 1–1.5 mm. long, glabrous; style very short, 0.2–0.3 mm. long, stigmas short,

notched; gland about 0.5 mm. long; scales oblanceolate, obtusish or acute, pale brown, nearly glabrous outside, thinly pilose inside, about 0.8 mm. long: staminate aments slender, spreading, 2–3 cm. long, 1 cm. wide; stamens 2, filaments glabrous, free; anthers short, obovate to nearly round, reddish or purplish; scales as in pistillate ament.

Salix Farrae Walpoleii is separated readily from the species by the pubescent-pilose young twigs, the broader, more obovate leaves, the longer and laxer aments, and the shorter styles. *Walpole's* no. 1624 in the United States National Herbarium is designated as the pistillate type. His no. 1742 has the best aments of any of the three staminate specimens seen and is designated as the staminate type. The variety flowers from about June 20 onward through July or early August, according to location. This willow rather closely resembles *S. balsamifera* (Hooker) Barratt, from which, however, it is readily separated by the entire leaves, seldom rounded and never cordate at base, the short pedicels, and somewhat shorter styles. Its nearest relative on the *S. cordata* side is *S. mackenziana* (Hook.) Barr., from which it is separated easily by the thin, entire, elliptic-obovate leaves, and more especially by the short pedicels. The variety is named for F. A. WALPOLE, since deceased, who collected several specimens of it in the vicinity of Port Clarence, near Cape Prince of Wales, Bering Strait, the most western locality at which it has been found. The specimens referred to it are cited later. So far as known, it is the only member of the section CORDATAE with an exclusively Arctic distribution.

ALASKA.—Vicinity of Port Clarence; north side and east end of Grantley Harbor, *F. A. Walpole* 1594, 3–4 ft. high, July 29, 1901 (N); rocky banks, northwest shore of Imunik Basin, *F. A. Walpole* 1624, 5–8 ft. high, July 30, 1901 (N, type); banks of Fuksuk Channel, *F. A. Walpole* 1742, 3–4 ft. high, August 5, 1901 (B, N); Cape Nome, *F. O. Blaisdell*, summer 1900; Fort Hamlin, Yukon River, to Bergman, Koyukuk River, Dall River, 75 miles above the mouth, *W. C. Mendenhall*, June 25, 1901 (N, two sheets); Valley of Alaskuk River, small willow, 2–4 ft. high, found along river, 30 miles above its mouth, *W. C. Mendenhall*, July 21, 1901 (N); along Help-me-Jack Creek, near camp, *W. C. Mendenhall*, common in river bottoms, about 5 ft. high, July 26, 1901 (N); Valley of Kobuck River, small bushy willow about 4 ft. high, on bank of small stream, *W. C. Mendenhall*, July 20, 1901 (N); Seward Peninsula, *A. J. Collier*, 1900 (N).

SALIX LASIOLEPIS **Bakeri** (v. Seem.), n. comb.—*S. Bakeri* von Seemen, Bull. Torr. Bot. Club **30**:635. 1903.—A shrub or small tree essentially like *S. lasiolepis* in most respects, except that the capsule is thinly pubescent, especially toward the apex. The

capsule, 5–6 mm. long, also appears to be slightly larger than in the species and the style slightly longer.

When VON SEEMEN described *S. Bakeri* he did not compare it with *S. lasiolepis* or mention that species in any way. He published two other species in the same paper, *S. franciscana* and *S. ormsbyensis*. In neither case did he indicate their relationships or mention other species in connection with them. We might infer either that American species were not well represented in the Berlin herbarium or that VON SEEMEN did not look them over. His description of *S. Bakeri* fits *S. lasiolepis* perfectly except in the one phrase "apex with short gray hairs" in reference to the capsule. All the evidence goes to show that the describer was unaware of *S. lasiolepis* rather than that he knowingly was segregating from it a new species with pubescent capsules. This variety is comparable to var. *puberula* under *S. commutata*.

Two specimens collected by *F. A. Walpole*, at Modoc Point, Klamath County (2198, 2200), on June 5, 1902 (N), are similar to the specimens cited later. The capsule in the Klamath specimens, however, is longer (6–8 mm.), much resembling that of *S. scouleriana*. I have considered these two, therefore, to be hybrids between *S. lasiolepis* and *S. scouleriana*. It is possible that the plants here referred to var. *Bakeri* are hybrids also, but this is less probable. One striking character in the Klamath specimens is the elongated pedicel, 1.5–2.5 mm. in no. 2198, which is longer than in either supposed parent.

CALIFORNIA.—Foothills near Stanford University, Santa Clara County, *C. F. Baker* 274, March 9 and May 10, 1902 (N, cotype); Berkeley, *W. L. Jepson*, March 24, August 15, 1891 (N).

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VESSELS OF THE GNETALEAN TYPE IN ANGIOSPERMS[1]

R. C. MacDuffie

(WITH PLATES XXIX–XXXII)

A common feature of Gnetales and Angiosperms is the possession of true vessels. The evolution of the vessel perforation and its typical form have long been matters of investigation. THOMPSON[2] has stated recently that the derivation and evolution of the vessel in Gnetales is distinct and different from that found in Angiosperms. On the other hand, SOLEREDER[3] and DEBARY[4] mention the existence among certain Angiosperms of the peculiar bordered pore which THOMPSON so definitely limits to the Gnetales. The present investigation, which covers a number of species of Angiosperms and Gnetales, confirms and extends the observations of SOLEREDER and DEBARY on Angiosperms and of THOMPSON on Gnetales. The writer finds it necessary, however, to differ from the conclusions of THOMPSON on Angiosperms.

Gnetales

In *Ephedra*, the lowest genus of Gnetales, primitive conditions of vessel organization are found. Fig. 1 is a section of wood taken in a primitive region near the pith. To the extreme left are the long slender tracheids with their characteristic pits, bordered and containing a torus. In the center are two large vessels which, in their several ways, show a distinct relation to and evolution from the tracheid condition. The vessel more to the left has pits of ordinary tracheary type at either end, except that they are somewhat enlarged in the vessel condition, but retain both border and

[1] Contribution from the Laboratories of Plant Morphology of Harvard University.

[2] THOMPSON, W. P., Independent evolution of vessels in Gnetales and Angiosperms. BOT. GAZ. **65**:83–90. 1918.

———, Anatomy and relationships of the Gnetales. 1. *Ephedra*. Ann. Botany **26**:1077-1104. 1912.

[3] SOLEREDER, HANS, Systematische Anatomie der Dicotyledonen, Stuttgart. 1899.

[4] DEBARY, H. A., Comparative anatomy of the vegetative organs of the Phanerogams and Ferns. Trans. by F. O. BOWER and D. H. SCOTT. Oxford. 1884.

torus. In the center of the same vessel, passing upward from the lower end, is one pit which retains its border but has lost the torus and membrane. The center of this vessel shows as many as five perforations which have gone a long way in evolution and have lost both membrane and torus. It is to be concluded that these are perforations highly specialized to carry on the vascular function. The vessel to the right has a precisely similar condition at either end, namely enlarged tracheary pits. Toward the center of this vessel from top or bottom are three pits in the first case, and two in the second which retain border and torus, but have reached distinctly the size characteristic of vessels. The eight more central pits retain a definite border, but each shows an absence of membrane and torus. This vessel is obviously less specialized, and therefore less efficient than the one previously considered; nevertheless it shows marked progress in the line of development. To the extreme right are typical tracheids, once again proving that these two vessels occur side by side with the elements from which they originate.

In *Gnetum*, the highest genus of Gnetales, conditions are especially interesting. Fig. 2 shows a longitudinal section, in rather low magnification, taken from the medullary region. The first vessel to the left has pits of the tracheary type at its top. These are many, crowded, and retain border and membrane, there being usually no torus in *Gnetum*. Toward the center the pits are somewhat enlarged, although still retaining the border. In the region of the perforation of the vessel there is a group of seven pits. These are distinctly larger than those on the side wall of the vessel and larger than those of most tracheids, and their borders are still distinct. The most interesting feature of this group, however, is found in the two lowest pits whose adjacent borders have broken down and show well defined fusion. This is the first example of pit fusion to be described, and is clear and convincing. Moreover, this is obviously a step higher than the conditions found in *Ephedra*, and foreshadows the more extensive fusion of pits to form a single large opening, which is the natural outcome from such conditions. In the same figure to the right are two large vessels in series. The higher vessel shows a large perforation resulting from pit fusion.

About this perforation is a well defined border, and except for a vestige of a cross wall that runs into it from the left, we should find here the simple large open perforation which is the result of complete fusion; in other words, the type characteristic of the more advanced species of *Gnetum*. The vessel below shows an imperfect perforation resulting from the more or less complete fusion of a number of large open bordered pits.

Fig. 3 presents a higher magnification of two large vessels, the one to the extreme left showing a group of four large tracheary pits arranged suggestively for fusion. To the right is a vessel with a single large opening as its perforation, this being the typical condition in more advanced species of *Gnetum*. The border is distinct, and by its slightly irregular outline, which shows especially well at the upper right side of the perforation, reveals its origin from a type like the vessel on the left in the same figure. Fig. 4 is a high magnification of an intermediate stage of fusion, showing the remains of a transverse process about to disappear.

Angiosperms

In Angiosperms the evolution of the vessel from the tracheid proceeds along the same lines as in Gnetales. Fig. 5 shows the organization of the mature wood in *Alnus japonica*. Here is seen the scalariform perforation characteristic of the Betulaceae and other presumably primitive Angiosperms. The pits, which are many and crowded, have fused in horizontal rows to form scalariform pits. The condition is seen even more clearly to be decidedly scalariform under higher magnification, as in fig. 6.

A section through the medullary region of *Alnus japonica* is shown in fig. 7. This is a rather low magnification, but shows clearly the primitive spiral and scalariform tracheids to the left. The three vessels to the right of these tracheids show all transitional stages from small pits to the scalariform perforations. The occurrence of this form of vessel perforation side by side with scalariform tracheids proves that it is indeed a primitive type for this genus of the woody Angiosperms. Fig. 8 shows these same vessels and tracheids under higher magnification. Fig. 9 is still another

high magnification of a vessel in *Alnus japonica*, in which the origin of the scalariform perforation from fusions of rows of pits is clear and convincing.

We pass now from woody Angiosperms to the consideration of the herbs and vines among Angiosperms, which in their vascular structures more closely resemble the conditions found in *Gnetum*, and show stages of perforation strikingly like those found in that genus. Fig. 10 is a section through the wood near the pith of *Potentilla palustris*. Several vessels are shown in the figure with a rather advanced development of the scalariform pits in the region of perforation. This condition resembles that found in the mature wood of *Alnus*. Fig. 11 is a section taken from the medullary region of *Potentilla monspeliensis*, an annual species. To the left are the characteristic spiral and scalariform tracheids of the protoxylem, and to the right are vessels with scalariform perforations on the end wall. Of these vessels, the one to the right shows a tendency at its lower end toward fusion of the scalariform pits. To the extreme right of the same figure is a vessel, low in the field, with the single large bordered pore characteristic of the mature wood of *Potentilla* as well as of the vessels of *Gnetum*. A further example of the close relation to the Gnetalean pitting is found in fig. 12, another section of the wood of *Potentilla monspeliensis*. To the left are two vessels in series. Both have the small pits grouped for fusion as in *Ephedra* and in certain species of *Gnetum* (figs. 1–3); in fact several of the pits have already fused in the higher vessel. To the extreme right is a vessel with a large *Gnetum*-like pore. Fig. 13, another section of *Potentilla monspeliensis*, shows three other vessels in the region of perforation. The vascular element to the left has again *Ephedra*-like pits grouped and fusing. The two vessels to the right in series have a curious *S*-shaped fusion of pits, quite out of keeping with any mode of origin save a haphazard union of pits. Fig. 14 shows part of the same field under higher magnification. It is clear that the two vessels here manifest the process of fusion of numbers of small pits. Fig. 15 is a high magnification of a similar condition in the same genus. Examples of like conditions might be indefinitely multiplied from

the study of this and other species of *Potentilla*. From the mode of perforations found in *Potentilla* it is seen that both the scalariform type and the *Gnetum*-like type, resulting from haphazard fusion, occur side by side and sometimes in the same species. It thus appears that both *Ephedra* and *Gnetum*-like types of perforation occur in this instance, and undoubtedly the bordered open pore has originated here from the grouped pits, either by horizontal or haphazard fusions. The possession of the scalariform type of perforation thus loses significance as a phylogenetic criterion and has only the importance of an anatomical detail. Further, the open bordered pore has often the same derivation in *Potentilla* and in other herbaceous Rosaceae as the similar bordered pore in *Gnetum*.

We pass now to the Geraniales, a group systematically remote from the Rosaceae. Fig. 16 shows a longitudinal section of the wood of *Pelargonium*. In the center is the region of perforation of a vessel, showing the bordered pore typical of the more advanced species of *Gnetum*. Even the border is clearly evident, a condition which THOMPSON apparently has failed to observe as occurring in the so-called porous perforation characteristic of the vessels of many Angiosperms, particularly (although not exclusively) those of herbaceous and liana-like habit. Fig. 17 shows another vessel of *Pelargonium* which illustrates an *Ephedra*-like perforation in this genus. There is obviously no difference here from the vessel perforation found in *Ephedra* except that the pits are small and both torus and membrane are always absent. There is no reason to believe that these pits are to fuse to form scalariform perforations, rather there is every evidence to infer a prospective haphazard fusion from the two or three instances of union manifested along the lower border of the perforation. This type precedes the open pore of fig. 16. Additional proof of this conclusion is supplied in fig. 18 from the same genus (*Pelargonium*). The vessel to the left has an interesting perforation. Small pits in the process of fusion surround an open bordered pore. When fusion is complete the enlargement of the central bordered porous opening will result. In the vessel adjacent to this is the large open bordered pore characteristic of the vessels of the Geraniales, and below it is

another similar perforation. Fig. 19 shows a higher magnification of the same vessel as presented in fig. 18. The details of border in the large central pore demonstrate the existence in Angiosperms of the *Gnetum*-like pore. Fig. 20 illustrates another vessel of *Pelargonium* showing two perforations in series. The upper perforation manifests a transitional stage of fusion. The high degree of magnification furnishes undoubted evidence that the complete fusion of pits will result in a large bordered perforation precisely as in *Gnetum*. Below is a bordered porous perforation.

Fig. 21 shows the partially pitted perforation of another vessel of *Pelargonium*. Fusion for the most part has already taken place, but enough small pits remain to establish a definite origin of the open bordered pore by *Gnetum*-like haphazard fusion. Fig. 22 shows a scalariform perforation in the same species of *Pelargonium*. The existence of this type, together with the bordered perforation derived from the fusion of *Ephedra*-like terminal pits, illustrated in the Rosaceae, shows again that the scalariform type of perforation is not exclusively present in or solely characteristic of Angiosperms. There is undoubted similarity between perforations of the Rosaceae and the Geraniales and those obtaining in *Gnetum* itself.

Fig. 23 shows two interesting vessels of the wood of *Tropaeolum* as a further illustration of the Geraniales. Both vessels have the *Ephedra*-like grouping of pits, although the size is obviously smaller than in that genus. Close scrutiny reveals the fusion to be haphazard-oblique and marginal, and not resulting in horizontal scalariform perforations. Most of the vessels in *Tropaeolum* have the *Gnetum*-like bordered terminal pore. Fig. 24 shows a section through the wood of *Clematis* species, an example of the Ranunculaceae. The margin of an open bordered perforation is shown, and around its inner edge is seen a fringe of haphazardly fusing pits. Vessels of the *Gnetum* type are practically universal in the Ranunculaceae.

Conclusions

Conditions similar to those illustrated for the Rosaceae, Geraniales, and Ranunculaceae are widespread among dicotyledonous Angiosperms, particularly those of herbaceous and climbing habit.

It seems unnecessary to exemplify further the occurrence of perforations identical with those characteristic of the Gnetales in the Angiosperms, since the examples furnished, which could be indefinitely multiplied, show that the vessels of Angiosperms can and often do originate precisely as in the highest group of the Gymnosperms, the Gnetales. It accordingly appears clear that THOMPSON'S assumption of a distinct origin for the Gnetales on the basis of a different mode of derivation of their vessels falls to the ground. This author has pointed out that the types of rays found in the Gnetales are strikingly similar in their mode of origin to those of the Angiosperms. He has further recently drawn attention to the nuclear fusions in the embryo sac of *Gnetum*, which he compares with the well known nuclear fusions in the female gametophyte of Angiosperms. It would appear, therefore, that far from demonstrating by his description of the mode of origin of vessels in *Gnetum* the separate derivation of the Angiosperms from the Gnetales, in reality this author has furnished additional conclusive evidence of their descent from a common stock. It is apparently clear from the present investigation that many herbaceous and vinelike Angiosperms, from the lowest to the highest groups, show types of vessel perforation identical with those found in the usually vinelike *Gnetum*. Even the Monocotyledons manifest very commonly the *Gnetum* type of vessel, which is further quite universal in the Compositae.

Summary

1. Vessels with scalariform perforations of the angiospermous type and bordered porous perforations of the *Gnetum* type occur side by side in the Rosaceae, being found even in the same species of *Potentilla*.

2. Similar observations are recorded for the Geraniales and Ranunculaceae, and these might be indefinitely multiplied from other herbaceous Angiosperms.

3. Recent statements that the types of vessels in the Gnetales and Angiosperms are distinct in their mode of derivation are accordingly without foundation in fact.

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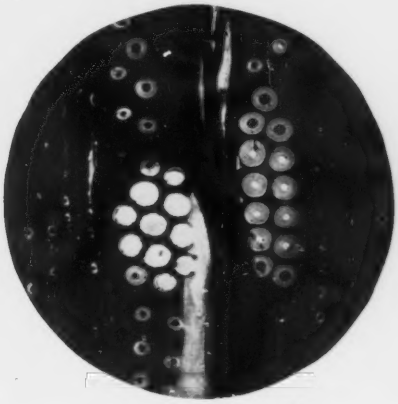

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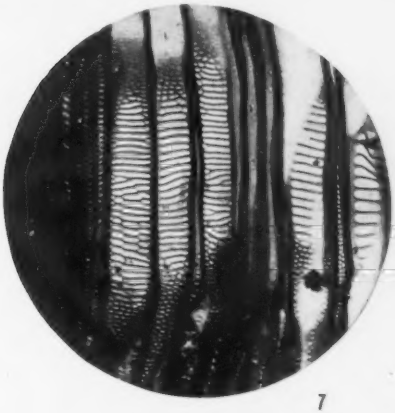

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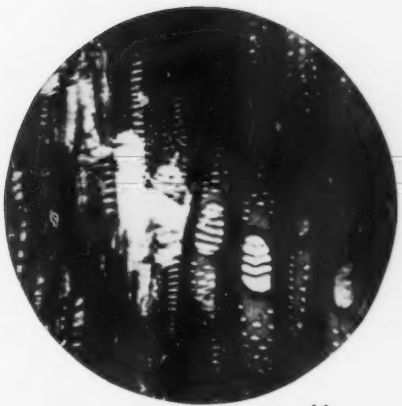

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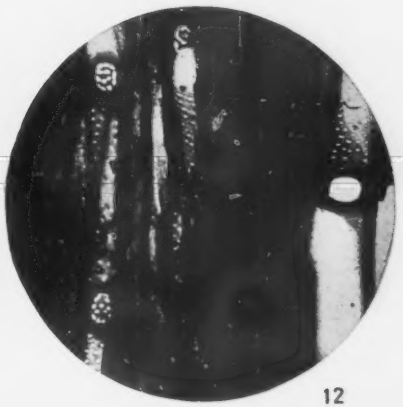

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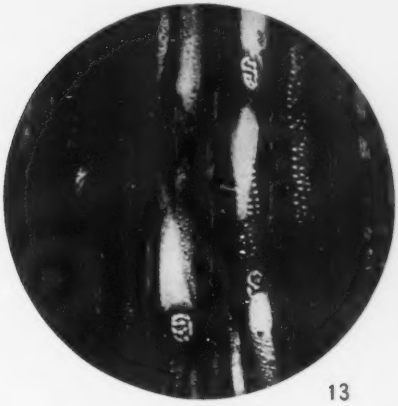

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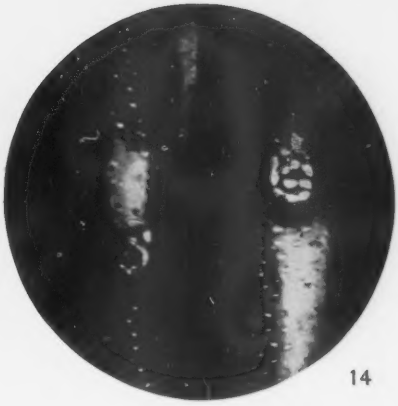

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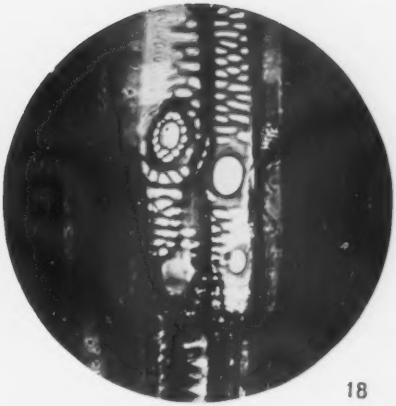

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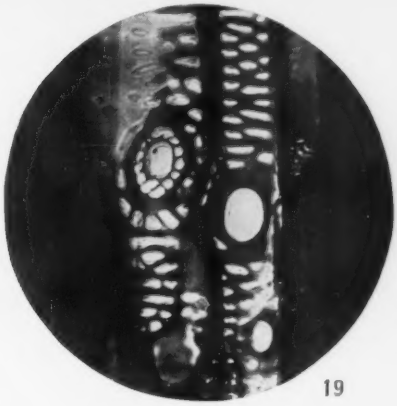

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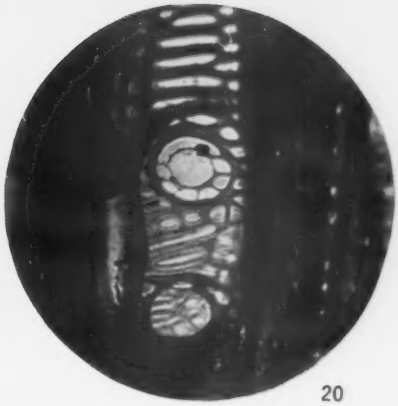

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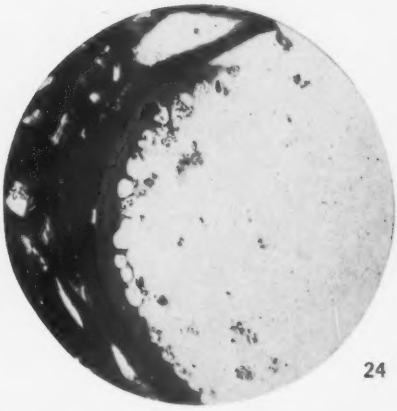

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MacDUFFIE on VESSELS

EXPLANATION OF PLATES XXIX–XXXII

PLATE XXIX

FIG. 1.—Radial section of wood of *Ephedra trifurca;* ×300.
FIG. 2.—Radial section of wood of *Gnetum* sp.; ×150.
FIG. 3.—Radial section of wood of *Gnetum* sp.; ×300.
FIG. 4.—Radial section of wood of *Gnetum* sp.; ×400.
FIG. 5.—Radial section of mature wood of *Alnus japonica;* ×200.
FIG. 6.—Radial section of mature wood of *Alnus japonica;* ×300.

PLATE XXX

FIG. 7.—Radial section of wood of *Alnus japonica* near pith; ×200.
FIG. 8.—Radial section of wood of *Alnus japonica* near pith; ×300.
FIG. 9.—Radial section of vessel of *Alnus japonica* near pith; ×400.
FIG. 10.—Radial section of wood of *Potentilla palustris* near pith; ×300.
FIG. 11.—Radial section of wood of *Potentilla monspeliensis* near pith; ×300.
FIG. 12.—Radial section of wood of *Potentilla monspeliensis;* ×200.

PLATE XXXI

FIG. 13.—Radial section of wood of *Potentilla monspeliensis;* ×200.
FIG. 14.—Radial section of lower part of same more highly magnified; ×400.
FIG. 15.—Radial section of another vessel of same species; ×400.
FIG. 16.—Radial section of vessel of *Pelargonium* sp.; ×400.
FIG. 17.—Radial section of *Ephedra* or *Gnetum*-like vessel perforation in *Pelargonium* sp.; ×400.
Fig. 18.—Radial section showing two vessels of *Pelargonium* sp.; ×200.

PLATE XXXII

FIG. 19.—Radial section of wood of *Pelargonium* sp., showing same two vessels more highly magnified; ×400.
FIG. 20.—Radial section of another vessel of same species; ×400.
FIG. 21.—Radial section of another vessel of same species; ×400.
FIG. 22.—Radial section of another vessel of same species; ×400.
FIG. 23.—Radial section of wood of *Tropaeolum* sp.; ×400.
FIG. 24.—Transverse section of wood of *Clematis* sp.; ×500.

EMBRYOGENY AND SPOROGENESIS IN REBOULIA HEMISPHAERICA

ARTHUR W. HAUPT

(WITH PLATE XXXIII AND ELEVEN FIGURES)

The present paper is a continuation of the writer's earlier morphological study of *Reboulia* (5). The systematic position of the genus and its phylogenetic relationships, as revealed by the structure and development of the gametophyte and sex organs, has already been discussed. To determine the affinities of *Reboulia* to other Marchantiaceae, as shown by the development of its sporophyte, was the purpose for which the present investigation was undertaken.

Material

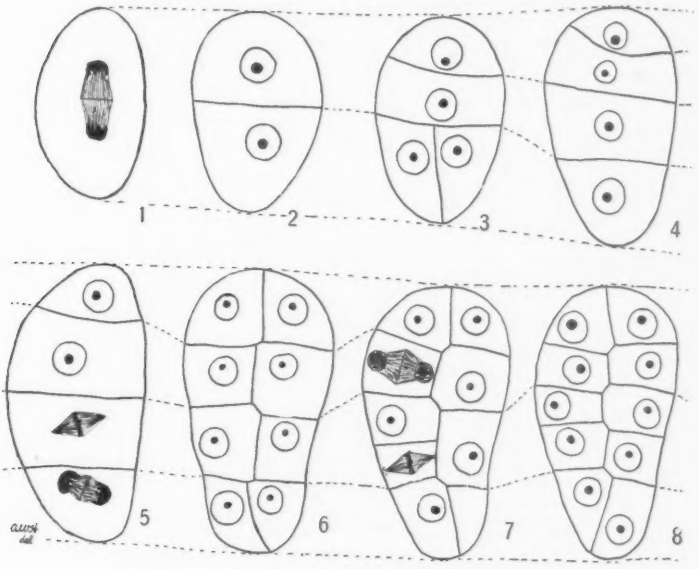
Material furnished by Dr. W. J. G. LAND for the earlier study, and collected by him at Rome, Indiana, served to illustrate a number of stages in the embryogeny. Most of the material, however, was collected by the writer during the autumn of 1919 and the spring of 1920 in the vicinity of Hamilton, Hancock County, Illinois. In this locality *Reboulia* occurs in abundance beneath moist ledges of sandstone. Material was also obtained from the region about Dakota, Illinois, through the kindness of Mr. EARL L. LAMBERT.

Embryo

The first division of the fertilized egg of *Reboulia* is invariably accompanied by a transverse wall (figs. 1, 2), the two segments being approximately equal in size. From a careful study of later stages the conclusion is reached that the epibasal segment gives rise to both the seta and capsule, while the hypobasal segment forms the foot. In a recent preliminary paper on *Reboulia*, WOODBURN (8) is in agreement with this interpretation. The next division results in the formation of a transverse wall in the epibasal cell which differentiates the cells which are to form the seta and capsule (fig. 3). A tier of 3 horizontally superimposed cells is thus developed. The lowest cell may again divide by a vertical wall (fig. 3), but more

commonly the uppermost cell divides again transversely before the appearance of the vertical wall in the basal cell, so that the young embryo consists of 4 superimposed cells (fig. 4). The latter condition has also been noted by WOODBURN.

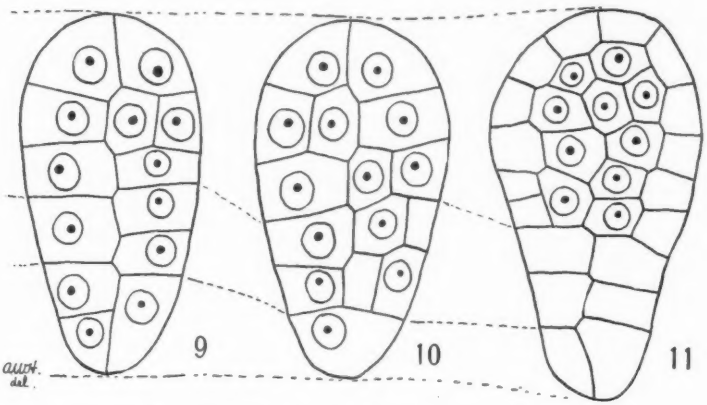
The formation of 3 transverse walls in the early embryo of *Reboulia* represents a behavior quite different from that of the other Marchantiaceae which have been studied. The appearance



FIGS. 1–8.—Stages in development of embryo; ×475.

of 2 vertical walls which intersect each other, after the first transverse division of the fertilized egg, has been shown by KIENITZ-GERLOFF (6) and DURAND (3) to be a constant feature of *Marchantia*. CAMPBELL (1) has demonstrated the regular formation of an octant in the early embryo of *Fimbriaria californica*, while CAVERS (2) has claimed that a similar condition prevails in *Reboulia*. KIENITZ-GERLOFF has also stated that the embryos of *Preissia* and *Grimaldia* develop like those of *Marchantia*, but his figures show no early stages, and are accordingly unconvincing. Following the

formation of the 3 transverse walls, vertical walls appear at right angles to each other in each horizontal tier (fig. 6), although the lowest cell may divide vertically before the appearance of the third transverse wall, as previously stated. These vertical divisions begin at the lower end of the embryo (fig. 5), a feature which is also noted by WOODBURN'S figures. Additional cross-walls then come in, and an embryo consisting of 5–7 tiers of cells is thereby formed (figs. 7, 8). This was a very common stage seen in the preparations. The additional transverse divisions occur chiefly in the upper part of the embryo. WOODBURN has observed the occasional formation of



FIGS. 9–11.—Older stages in embryogeny; ×475.

a triangular-shaped apical cell in the young embryo, and often of both triangular apical and basal cells. The writer has seen stages similar to those figured by WOODBURN, but found that the triangular form of the uppermost cell invariably resulted from an obliquely cut section. A truly median section has never revealed the presence of a triangular apical cell.

With the definite establishment of the vertical walls in the embryo, both transverse and vertical divisions occur chiefly in its upper portion (fig. 7, 9, 10), and finally the sporogenous tissue is delimited from the amphithecium (fig. 11). Further development is typical of that of other Marchantiaceae which have been investigated.

With the development of the sporogenous tissue and the cells of the foot, the young sporophyte gradually assumes a dumb-bell shape. The seta remains short throughout the entire history of the sporophyte. The calyptra, formed entirely from the venter of the archegonium, is 3–5 cells thick in this dumb-bell-like stage of the sporophyte. As development proceeds, the margins of the receptacle lobes grow up around the sporophyte to form a simple 2-valved involucre. No perianth is developed, as in certain other genera of the Marchantiaceae. The receptacle stalk is very short at a stage in which the sporophytes are developed as far as has been described, and they pass the winter in this condition.

Sporogenesis

In the early spring, about the last week in March in the region where this material was collected, the receptacle stalk begins to elongate, and further development of the sporogenous tissue takes place. In the early spring the sporogenous cells give no indication of which are to form spore mother cells and which elaters (fig. 12), but by the first part of May the walls separating the protoplasts of the sporogenous tissue break down and form an abundance of mucilage, and the young spore mother cells and elaters are clearly differentiated (fig. 13).

A striking feature of the sporogenesis of *Reboulia* is shown by the fact that the spore mother and elater primordial cells are derived from the undifferentiated sporogenous tissue by the same number of cell divisions. Thus an elater is not homologous with a row of spore mother cells, as in *Marchantia*, but with a single spore mother cell. Potentially sporogenous tissue is thus diverted to form elaters later than in *Marchantia*, and in this respect the sporophyte of *Reboulia* is primitive.

With the breaking down of the sporogenous cell walls, the protoplasts of the young spore mother cells become withdrawn within the cell cavities and assume an amoeboid form, while those of the young elaters become elongated (fig. 13). This behavior was constant in all of the preparations examined, and in material collected in both of the localities in Illinois to which reference has been made.

Miss McCormick (7) has shown in *Symphyogyna* that the spore mother cells assume an amoeboid form in connection with the development of the 4 lobes which characterize the spore mother cells of the Jungermanniales, and the same behavior has been observed in *Pallavicinia* (4). The assumption of an amoeboid character by the young spore mother cells of *Reboulia*, in which no lobes develop, clearly demonstrates that this behavior is not necessarily related to the formation of lobed spore mother cells.

With the gradual dissolution of the old spore walls, the spore mother cells lose their amoeboid form and become globular, gradually growing larger and becoming increasingly more dense by the accumulation of food material (figs. 14, 15). Thus the writer is inclined to regard the amoeboid development as a feature related to the nourishment of the spore mother cells. Their increase in size and globular form is certainly not due to the release of pressure upon the cells of the sporogenous tissue occasioned by the increased size of the capsular cavity, for no such enlargement or acquisition of food material is shown by the elaters.

The mucilaginous substance around the spore mother cells and elaters presents a foamlike appearance as these changes are going on, and becomes increasingly less dense. Both the spore mother cells and elaters form a new cellulose wall after the former have reached their maximum size (fig. 15). The new spore wall around the spore mother cells becomes thick and is differentiated into a thin intine and a heavy exine. Their protoplasts are now extremely dense, so that even in sections cut to a thickness of 3 μ it is very difficult to study nuclear details.

With the development of the walls in the spore mother cell to form the tetrad, a thin epispore is laid down (fig. 16). The elaters, which elongate considerably as the spore mother cells develop, have merely a thin cellulose wall when the tetrad stage in sporogenesis is reached, and their protoplasm is slightly withdrawn inside of the cell cavity.

With the separation of the spores from their tetrads, all of the mucilage is gone. The epispore develops prominences by a process of outbulging (fig. 17), so that the mature spore when seen from the surface is described as having a thick "tuberculate" epispore.

The protoplasm of the elaters becomes further withdrawn from the cell wall, and a double spiral band appears in the form of a local thickening on the inside of the elater wall. Finally all of the protoplasm is lost, as its substance seems to contribute to the further development of the spiral band.

The relation between the protoplasmic contents of the elaters and the formation of their spiral band was studied in all available stages in their development. In no case was a behavior observed such as has been described by CAMPBELL (1) for *Fimbriaria californica:*

> The elaters are at first elongated thin-walled cells with a distinct although small nucleus, and nearly uniformly granular cytoplasm. As they grow the cytoplasm loses this uniform appearance, and a careful examination, especially of sections, shows that the granular part of the cytoplasm begins to form a spiral band, recalling somewhat the chlorophyll band of *Spirogyra*. This is the beginning of the characteristic spiral thickening of the cell wall, and while at first irregular, the arrangement of the granular matter becomes more definite, and following the line of this spiral band of granules in the cytoplasm, there is formed upon the inner surface of the wall the regular spiral band of the complete elater.

The mature elaters average slightly over 1.0 mm. in length, the longest one measured being 1.36 mm. and the shortest 0.94 mm. The mature spores average 70–80 μ in diameter. The mature sporophyte reaches a length of 1.6–2.0 mm. The capsule is oval or slightly obovate; its wall is but 1 cell thick except near the apex, where a cap 3 or 4 layers of cells in thickness is formed. The outer wall cells develop simple annular and half-ring fibers. Dehiscence of the capsule was not observed, but it is probable that the apical cap comes off. The seta of the mature sporophyte is comparatively very short, and the foot is bulbous, never anchor-like.

Summary

1. The embryo of *Reboulia* develops without the formation of an octant stage characteristic of certain other Marchantiaceae.

2. The first transverse wall in the fertilized egg separates the cell which is to form the foot from that which is to form the seta and capsule. Four horizontally superimposed cells are usually formed, each new division occurring in the outermost segment. Of

these the lowest cell forms the foot, the next one the seta, and the upper two the capsule.

3. The sporogenous tissue is formed relatively early in the history of the sporophyte.

4. In the development of spore mother cells and elaters the walls around the sporogenous cells become mucilaginous, the protoplasts of the former assume an amoeboid form and finally become large and spherical, while those of the latter are slender and elongated. · A new cell wall is laid down around both spore mother cells and elaters.

5. The assumption of an amoeboid form by the young spore mother cells is a feature related to their nutrition.

6. An elater in *Reboulia* is homologous with a single spore mother cell, and not with a row of them.

7. The exine and intine are differentiated in the tetrad stage, and the epispore has begun to develop. The formation of a double spiral band on the elaters is accompanied by a condensation and ultimate disappearance of the protoplasm.

8. The short seta and bulbous foot are primitive features of the genus.

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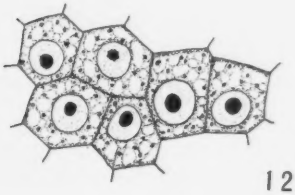

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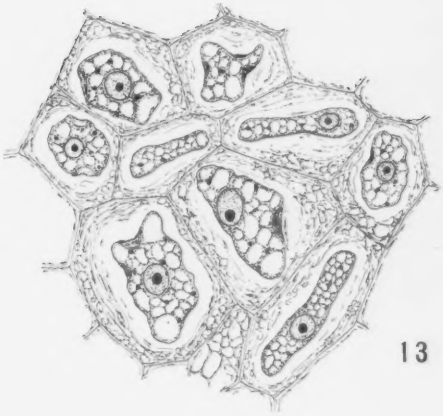

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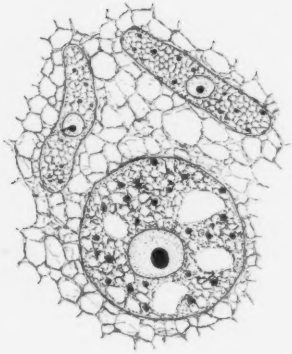

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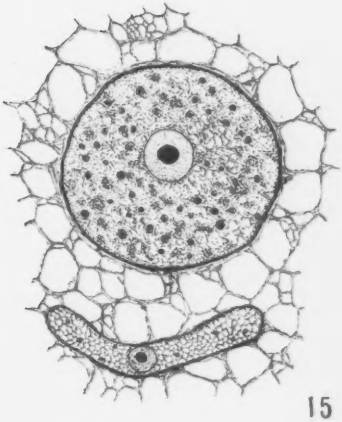

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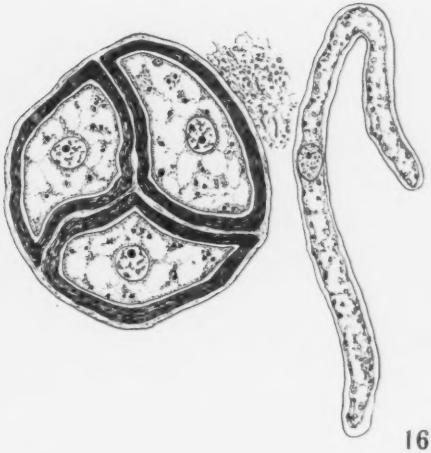

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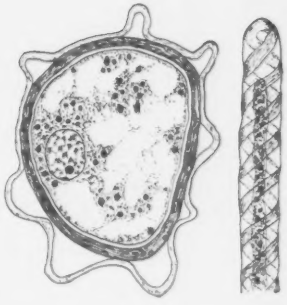

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HAUPT on REBOULIA

EXPLANATION OF PLATE XXXIII

FIG. 12.—Sporogenous tissue; ×720.

FIG. 13.—Young spore mother cells in amoeboid stage and young elaters; ×720.

FIG. 14.—Older stage showing development of cell walls around spore mother cells and elaters; ×720.

FIG. 15.—Older stage of same; ×720.

FIG. 16.—Spore tetrad showing development of spore coats and elater; ×720.

FIG. 17.—Nearly mature spore and elater showing development of epispore on former and double spiral band on latter; ×720.

DIAMETER GROWTH IN BOX ELDER AND BLUE SPRUCE

C. F. KORSTIAN

(WITH THREE FIGURES)

It is the common belief that trees grow throughout the greater part of the vegetative period, the commonly called "growing season," which is roughly defined as being limited to the period from the last killing frost in the spring to the first killing frost in the fall, when the broad-leaved hardwoods such as maple, ash, and aspen show their autumnal colors. In the Rocky Mountain forest region this period comprises from 75 to 100 days. Until recently little was known as to the exact time at which trees actually make their diameter growth. Neither has the course of growth nor the formation of the annual rings or cones of wood been measured until recently.

About twenty-five years ago FRIEDRICH (2), an Austrian forester, devised instruments capable of measuring the daily growth in diameter of trees. Somewhat later he improved his accretion autograph, as it was called, by adding an electric attachment which recorded the growth in the investigator's office. He would entertain his visitors by telling them that while they could not hear grass grow, they could not only see but hear the tree in the park grow, the increase in the periphery being announced by the sounding of a signal.

In 1918 MACDOUGAL devised a new instrument for recording in minute detail the daily and seasonal growth and all changes in the size of the trunk of a tree. The instrument is called a dendrograph. The essential part of it consists of a yoke composed of slotted bars of some alloy, such as bario or invar, which has a very low temperature coefficient. This is held in place by upright pieces of brass wire seated in small brass plates, which afford flexible supports capable of uniformly adjusting any tension which may be developed. These plates are clamped to a belt of wooden blocks hinged together and fastened securely to the tree, serving

as a rigid support for the instrument. As this belt comes in tangential contact with the tree at only a few points, it interferes very little with its normal growth. The recording apparatus consists of a drum carrying a record sheet, the drum being rotated by clock work. In order to minimize the effect of the shrinkage and expansion of the bark, it is rasped or shaved down so that a very thin layer of cork covers the living inner bark on small spots just large enough to give suitable bearings under the contact screw and under the end of the bearing lever. Changes in the diameter of the tree trunk, that is, between the contact screw on the opposite side of the tree and the arm of the bearing lever, are accurately traced on the sheet of record paper on the drum by the recording pen. In this way a continuous curve is traced on the revolving drum as it passes beneath the point of the pen, the position of which is gradually changed as the tree trunk expands in the process of growing. The instrument is protected from the weather by a tin cover attached to the tree. The clock requires winding and the record sheet must be changed at least every seventh day. When the instrument is once properly adjusted it requires no further adjustment except such as may become necessary owing to the growth of the tree. Fig. 1 shows the dendrograph on a blue spruce tree, with tin cover removed to show the recording mechanism.

FIG. 1.—MacDougal dendrograph in operation on a blue spruce, showing encircling belt of wooden blocks and yoke of invar, but with tin cover removed to show recording mechanism.

During the spring and summer of 1920 the writer had the privilege of operating one of MACDOUGAL'S dendrographs in cooperation with him. Because of the backward season in the mountains, the instrument was placed on a specimen of *Acer Negundo* in the city of Ogden, Utah, on April 1, 1920, for the purpose of determining when growth actually begins in this species. A period of unusually cold stormy weather followed the installation of the instrument, during which quiescence and alternate shrinkage and enlargement were recorded. The tree showed some enlargement April 10–14, which, however, did not continue during the following four days when high winds prevailed. Diameter growth did not properly begin until May 19. The buds were just beginning to swell on April 1. By April 27 practically all of the leaves had unfolded, and on May 5 they were about one-fourth full size. The leaves had reached about one-half their natural size before the main period of growth began on May 19.

Fig. 2 shows the daily march of the diameter changes. In order to afford a closer correlation, the march of the daily mean temperature of the air and of the cortical layer adjacent to the cambium or the zone of living tissue where the diameter growth actually occurs is plotted in the lower part of the figure. The greatest and smallest diameters reached during the day are plotted in the upper graph to show the diurnal variations. These diurnal changes apparently vary to some extent with the range in temperature. On cool cloudy days with relatively warm nights, which have small temperature ranges, the diurnal change in the diameter is slight, while on warmer clear days with cool nights, having a great diurnal temperature range, the diurnal shrinkage or expansion may amount to as much as 0.5 mm., indicating a direct temperature relationship. Moisture conditions are not considered among the critical factors causing the commencement of growth in the spring, because the soil is abundantly supplied with moisture from the melting of the winter snows and from the spring rains, until considerable growth has been made and fairly high temperatures obtain. As might be expected, there is a somewhat close correspondence between the trend of the two graphs, although the cambial temperature does not usually attain the extremes reached by the air temperature.

On June 7 the dendrograph was moved to the Cottonwood Nursery, twenty-five miles southeast of Salt Lake City, Utah, and placed on a specimen of *Picea Parryana* growing in the nursery grounds at an elevation of 7400 feet. At this time the spruce buds were bursting open and diameter growth was already under way,

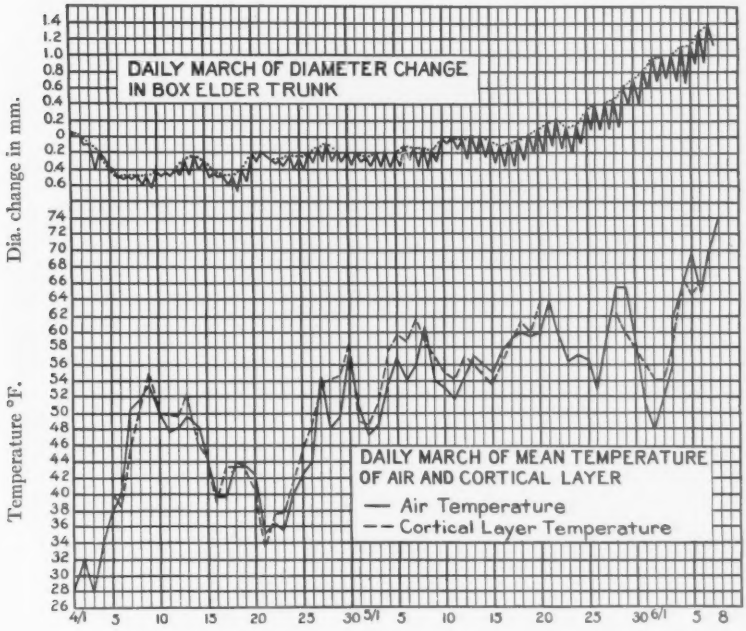
DAILY MARCH OF DIAMETER CHANGE IN BOX ELDER TRUNK
Dia. change in mm.
Temperature °F.
DAILY MARCH OF MEAN TEMPERATURE OF AIR AND CORTICAL LAYER
— Air Temperature
-- Cortical Layer Temperature
4/1 5 10 15 20 25 30 5/1 5 10 15 20 25 30 6/1 5 8

FIG. 2.—Daily march of diameter change in box elder trunk, daily mean temperature of air and cortical layer adjacent to cambium; Ogden, Utah, April 1–June 8, 1920.

as indicated by fig. 3, although it is not probable that much growth had taken place before the record began. Growth continued for slightly more than five weeks, except for two rest periods of two days each (June 19–20 and June 26–27). The shrinkage noted on June 9 and 10 may be a rest period, or it may possibly be due to a shrinkage occasioned by the drying out of the thin layer of cortical tissue after the main portion of the outer bark had been removed. In addition to the mean daily temperatures of the air and the cortical layer adjacent to the cambium, the mean daily

temperature of the soil at a depth of 12 inches is also shown in the same figure for comparative purposes. No direct correlation between the march of diameter growth and current temperatures was found. A careful study of the graphs leads to the inference

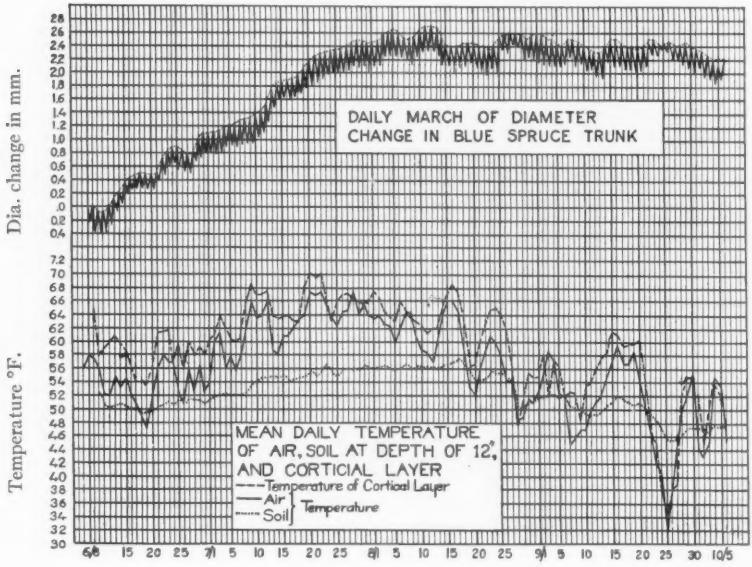
Dia. change in mm.
Temperature °F.
DAILY MARCH OF DIAMETER CHANGE IN BLUE SPRUCE TRUNK
MEAN DAILY TEMPERATURE OF AIR, SOIL AT DEPTH OF 12", AND CORTICIAL LAYER
---Temperature of Cortical Layer
——Air
-----Soil
Temperature

FIG. 3.—Daily march of diameter change in blue spruce trunk, daily mean temperature of air, soil at depth of 12 inches, and cortical layer adjacent to cambium; Big Cottonwood Canyon, 25 miles southeast of Salt Lake City, Utah, June 8–October 6, 1920.

that the growth response lags behind the temperature, a marked drop in the temperature causing a decrease in or even a cessation of growth[1]. HARTIG (4), as a result of extensive investigations, advanced the theory that the awakening of cambial activity was

[1] Since writing the preceding, an interesting temperature relationship was observed on a blue spruce tree growing on the writer's lawn in Ogden, Utah. On May 12, 1921, the buds on the north side of the tree had swollen and were just beginning to open, while on the south side practically all buds were open and new growth of 3–5 cm. had taken place on the tips of the branches. This difference in the inception of growth is believed to be due to the higher temperatures to which the buds on the south side of the tree were subjected.

dependent upon temperature, and that soil temperature, insolation, and the thickness of the bark were influential factors also.

GROSSENBACHER (3) has reviewed the varied and rather contradictory literature concerning radial growth in trees, the time of beginning and ending of cambial activity, and the factors thought to determine its distribution. He found a rather general agreement that, in our zone, wood formation generally ceases by mid-August, while that of the phloem continues practically to the end of the vegetative season. HARTIG (5) concluded that cambial activity first began in the youngest twigs and then gradually proceeded downward. HASTINGS (6) found that radial growth commenced first behind the opening terminal buds in broad-leaved trees and proceeded toward the base. By the time the five to six-year branches were forming new wood, radial growth had become general all over the trees. In the case of pine radial growth apparently commenced on the two or three-year old portions of branches before the buds opened. Growth started on the two-year pine branches possibly because the leaves were retained two years, for it was noted that in hemlock, where the leaves were retained six to seven years, radial growth appeared to have started first on six-year old branches. In *Taxodium distichum* radial growth started first just behind the opening terminal buds, as in broad-leaved trees, in which diameter increase did not begin until the buds had opened. REICHE (8) also noted that radial growth of trees in Chile began after the buds burst, and that it did not occur unless bud development preceded it. BUCKHOUT (1) reported diameter increase in *Larix europaea* to be practically coincident with the formation of new leaves.

KNUDSON (7), as a result of several years of investigation, including microscopical studies, found that the development of xylem in *Larix laricina* began a month later than the commencement of leaf formation, and ascribed BUCKHOUT'S observed diameter increase mainly to a preliminary swelling of the tissues. From his results and those of other investigators, KNUDSON believes it probable that in general diameter growth does not begin until the leaves have developed and have become sufficiently active photosynthetically to supply the requirements of rapid cell formation. The reserve food materials stored up in the autumn are probably

largely utilized in leaf and also in blossom formation, when the latter precedes leaf formation.

The most interesting fundamental principle of growth exhibited by the records obtained from the box elder and blue spruce trees is that growth evidently does not begin in deciduous hardwood trees and in evergreen conifers at the same time. These observations in general agree with the conclusions of KNUDSON. It would appear reasonable to assume that diameter growth proper, as distinguished from any preliminary swelling of the tissues which might occur, may be delayed until the new leaves are sufficiently developed to elaborate the supply of food needed for the rapid growth which takes place. The supply of stored food which is present in the spring is largely consumed in the formation and development of the new crop of leaves to a stage when they can supply the quantity of elaborated food necessary for the growth processes. On the other hand, the evergreen conifers, having an adequate amount of living leaf tissue, are capable of supplying the requisite materials for growth as soon as growing temperatures are reached in the spring. In other words, the inception of diameter growth in evergreen conifers may practically be simultaneous with the bursting of the buds, while in deciduous-leaved hardwoods it may be delayed until the new leaves have attained a sufficient size to manufacture their own food.

It will be noted that the march of diameter growth is interrupted by rest periods of rather short duration. These rest periods are held to be essential for the maintenance of the proper health and optimum efficiency of the vital activities of the tree.

Figs. 2 and 3 combined outline the seasonal course of diameter growth as follows. It begins slowly, and after a variable period increases rapidly by leaps and bounds, alternating with rest periods, until a maximum rate is attained; after a short time it gradually decreases to a minimum, and then ceases altogether, when the usual alternate shrinkage and expansion (due to the changes in temperature and moisture conditions of the tree trunk) are exhibited.

Aside from the scientific consideration of the fundamental principles of growth, the use of such an instrument as the dendro-

graph has several practical applications. In connection with the measurement of permanent sample plots, the question has often confronted the forester as to when diameter growth occurs and whether it is coincident with height growth. It is very frequently much more desirable from the standpoint of expediency to measure the plots during the summer than in the fall and winter, when the trees are known to be in a dormant condition. An economic consideration is in connection with the peeling of logs and poles, where this practice is necessary. It is a well known fact that peeling is most easily done when the sap is flowing freely, which is also the time of the greatest growth activity. It can be seen, therefore, that a determination of the beginning and ending of the period of actual growth will suggest the time during which peeling can be accomplished most easily. An accurate record of the march of diameter growth, when correlated with the different site factors, will aid materially in the determination of those factors most influential in conditioning tree growth, which is necessary as a basis for a rational silvicultural practice.

UNITED STATES FOREST SERVICE
OGDEN, UTAH

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BRIEFER ARTICLES

ALFRED GABRIEL NATHORST

(WITH PORTRAIT)

ALFRED GABRIEL NATHORST was born on November 7, 1850, and died at Stockholm on Januray 20, 1921. Three years before his death, having reached the age limit of active service, he retired from the directorship of the Paleobotanical Museum of the Swedish Academy, a post which he had held for many years to the great benefit of his favorite science. In 1917 he wrote, "I am growing old and my health has been much weakened in consequence of a disease of the heart for the last one and a-half years"; again in October, 1919, "I have not been able to work seriously since 1916, but now I hope to have regained so much of my strength that I may complete an additional work on the Lower Carboniferous at Spitzbergen." This hope was fulfilled, and in 1920 was published the last of a remarkable series of memoirs on Arctic floras.

NATHORST'S contributions to knowledge cover a period of fifty-one years. His first paper, on Cambrian rocks of Scania, was published in 1869. The range of subjects is exceptionally wide, and everything he touched he illuminated.

A few years before his death, NATHORST had the satisfaction of seeing his beloved collections installed in a new and worthier home outside the city, under the guardianship of his former pupil and assistant, Dr. HALLE, to whose able hands he was well content to intrust the reputation of the museum as a center of paleobotanical research. In

1905 NATHORST visited several scientific institutions in England and on the continent, in company with a Swedish architect, for the purpose of obtaining information in preparation for the new building, toward the erection of which parliament subsequently voted £140,000. Three years later he wrote, "I am happy to have founded this museum for the sake of paleobotany and my successors."

It was my good fortune on two occasions to spend several days in the old museum with NATHORST, and it will always be the small and crowded rooms in the heart of Stockholm that some of us will remember with feelings of admiration, gratitude, and affection. The accompanying photograph, taken by my colleague W. HANISHAW THOMAS, and regarded by NATHORST as the best of his portraits, shows the director at work in his private room. Other museums may be larger and more imposing, but none contain as many treasures or form a more impressive monument to the life-long devotion of a conscientious and wholehearted student of nature.

NATHORST was universally regarded as a master in paleobotany; a geologist of the first rank; an Arctic explorer whose extended geological and geographical researches in Spitzbergen, Bear Island, King Charles Land, Ellesmere Land, and other regions in the course of several expeditions, notably that of 1898–1899 of which he was the scientific leader, were fruitful in results of the greatest importance; and an expert systematic botanist. He was an exceptionally all-round naturalist, in whom were happily combined sound learning, breadth of view, and a natural modesty. Although seriously handicapped by his almost complete deafness, he was intensely happy in his work. He spoke English and German with surprising fluency and correctness, and wrote in both these languages and in French. In one of his letters he said, "It is easier for me to write in German than in English, but I think it would have been better if I had published my papers in English, as paleobotany is now (1908) chiefly and with best results studied in England and America."

In 1872, at the age of twenty-one, he paid his first visit to England, when he met Sir CHARLES LYELL, whose *Principles of Geology* awakened his love for that science. In 1907 he came as a delegate to the centenary of the Geological Society of London, and in 1909 to the Darwin Celebrations at Cambridge, a visit which he thoroughly enjoyed in company with Professor ZEILLER of Paris, of whom he afterward spoke as "our dear, noble, and lamented friend." NATHORST never visited the United States. In 1914 he wrote, "I really should like to study

the flora of eastern North America in connection with the Tertiary flora of Spitzbergen." He was deeply interested in Dr. WIELAND'S work on the fossil Cycads, for which he had a great regard, although he did not approve of the application of the term Cycad to the fossil stems which he maintained differed too widely in the fertile shoots from the Cycadales to be placed in that group. NATHORST'S own works on the Cycadophyta (a class designation which he instituted) not only added greatly to our knowledge of the extinct types, but stimulated other workers in the same field.

It is impossible in a short article to give an adequate idea of NATHORST'S contributions to paleobotany. Among his better known researches are those on Arctic floras from Devonian to Tertiary, his series of *Paleobotanische Mitteilungen* in which many new types, notably Devonian and Rhaetic genera, are described, his thorough study of the Rhaetic and Liassic floras of Scania, the series of papers on supposed fossil algae which were revolutionary and had a far reaching and salutary influence, his work on the distribution of Arctic plants during the Glacial period inspired by his first-hand knowledge of recent Arctic plants, his numerous contributions to our knowledge of Mesozoic floras in widely separated parts of the world, from Graham Land and the Falkland Islands to the new Liberian Islands, and his stimulating papers on British fossil plants. Although he did not concern himself with the investigation of petrifactions, his skilful use of improved methods which he invented for examining the mummified cuticles of impressions led to astonishing results.

NATHORST had the true scientific spirit. His work was based on a firm foundation of accurate and wide knowledge of botany and geology; he recognized the limitations of his material and never ventured to deal with matters on which he was not competent to speak with the authority of a specialist. In 1895 he wrote in one of a long succession of most helpful letters, "The chief rule in dealing with fossil plants is that one ought to say precisely as much as the material allows, neither more nor less. This is the ideal, but one cannot help sometimes saying a little too much in consequence of what one besides (that is, beyond the available evidence) does believe!" He strongly deprecated the overconfidence of some paleobotanists and their departure from a wholesome skepticism. In 1919 he wrote in a letter, "The longer I live, the more my skepticismus is developed, although my projected great work on *Skepticism in paleobotany* in twelve volumes will probably never appear!" He took a delight in helping others with kindly encourage-

ment and frank criticism. For him, purely destructive criticism had no charm; he always took pains to be stimulating and constructive. His sincerity and generosity inspired confidence and affection. He had a keen sense of humor, and with a boyish sense of fun he combined the mature judgment and cautious outlook of a philosopher. He loved to write and talk of his work: "You can hardly imagine how isolated I am here. My correspondence with friends and fellow-workers has been a great source of joy and satisfaction."

It was a privilege to know NATHORST. His achievements won for him a preeminent position among his colleagues, but one thinks of him, now that he has gone, not so much as the stimulating teacher that he unquestionably was, but more especially as a very human friend, the memory of whose generous spirit and affectionate regard is a precious possession.—A. C. SEWARD, *Cambridge, England.*

CURRENT LITERATURE

NOTES FOR STUDENTS

Applied ecology.—Increasing attention is being paid to the application of ecological principles to problems in plant and animal agriculture, horticulture, and forestry. Among the more important recent papers in this field are three contributions by SAMPSON,[1] and one by SAMPSON in conjunction with WEYL.[2] The first of these is an attempt to show a correlation between climate, vegetative associations, and crop production. Stations for instrumental work were established in the Manti National Forest of Utah at three different elevations, one in the oak-brush association which ranges from 6500 to 7800 ft. in altitude, a second in the aspen-fir association which ranges from 7500 to 9500 ft., and a third in the spruce-fir association which ranges from 9000 to 11,000 ft. The plants used in the experiments were field peas, Kubanka wheat, and the mountain brome grass (*Bromus marginatus*). Measurement was made of transpiration, wind velocity, temperature, rainfall, evaporation, sunshine, and barometric pressure, and comparisons were made with plant growth and water requirement. The number of growing days varies from 120 at the lowest to 70 days at the highest station. The greatest rainfall is at the middle station, being about twice that of the station below. The evaporation is greatest at the lowest station, but is almost as great at the highest station, owing to wind velocity. The necessary effective heat units for wheat and field peas exist only at the lowest station, where the water supply is inadequate unless supplied artificially.

SAMPSON'S paper on plant succession in relation to range management is a peculiarly apt illustration of the importance of ecological principles in the treatment of range lands. To most agriculturists it would seem a far cry from an academic study of plant succession to the practical treatment of range land and pasture, but SAMPSON makes it very clear that the relation between the two is fundamental. Stockmen have generally recognized that overgrazing is a common result of their practice, but they have for the most part been unable to detect overgrazing in time to stop the damage. SAMPSON has

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[1] SAMPSON, ARTHUR W., Climate and plant growth in certain vegetative associations. Bull. 700, U.S. Dept. Agric. pp. 72. *figs.* 37. 1918.

———, Plant succession in relation to range management. Bull. 791, U.S. Dept. Agric. pp. 76. *pls.* 2. *figs.* 26. 1919.

———, Effect of grazing upon aspen reproduction. Bull. 741, U.S. Dept. Agric. pp. 29. *pls.* 5. *figs.* 7. 1919.

[2] ———, and WEYL, L. H., Range preservation and its relation to erosion control on western grazing lands. Bull. 675, U.S. Dept. Agric. pp. 35. *pls* 6. *figs.* 8. 1918.

shown that grazing results in retrogression, the more stable or climax forms being gradually eliminated and their place being taken by plants characteristic of more primitive successions. The key to the situation, therefore, is the invasion of the more stable or climax formations by relatively pioneer forms. If such invasion is detected in time, grazing may be reduced or wholly abandoned for a time, thus giving the more desirable species characteristic of the higher successional stages an opportunity to reestablish themselves. The region under consideration in this paper is the neighborhood of the Great Basin Experiment Station in the Manti National Forest. Here four major successional stages are recognized: the first or early weed stage, characterized by ruderals; the second or late weed stage, with foxglove (*Pentstemon procerus*), sweet sage (*Artemisia discolor*), and yarrow (*Achillea lanulosa*) as leading species; the mixed grass and weed stage, with porcupine grass (*Stipa minor*) and yellow brush (*Chrysothamnus lanceolatus*) dominant; and the subclimax or wheat-grass (*Agropyron* spp.) stage. The wheat-grasses constitute the climax herbaceous cover and are desirable range grasses. Overgrazing nduces the appearance of species characteristic of the next lower stage, and continued overgrazing may even result in the appearance of the more primitive weed stages. The most representative indicator of retrograding wheat-grass land is *Chrysothamnus*. The *Stipa-Chrysothamnus* stage is equal or slightly superior to the *Agropyron* stage for range land purposes. Retrogression to the *Pentstemon-Artemisia-Achillea* stage is distinctly undesirable, although sheep do well here. Retrogression to the first or ruderal stage may be disastrous. If grazing is permitted here, all vegetation may disappear and finally the soil itself, through the action of erosion, in which event recovery is difficult or even impossible. In the treatment of the different vegetational stages, the writer considers in detail the conditions of growth and reproduction, the soil water content, the root relations of the characteristic species, the effect of disturbing factors, palatability, and forage production. All-in-all this is one of the most important papers in the field of applied ecology, and may well serve as a model to investigators everywhere.

The studies resulting in SAMPSON'S paper on the effect of grazing on aspen reproduction were also carried on in the Manti National Forest. This paper recommends that an attempt be made to work out a proper balance between the production of meat and timber. As the aspen does not reproduce effectively in its own shade, it is recommended that the timber be cleancut, and that the new growth be exempted from grazing or be grazed moderately by cattle rather than by sheep, which are much more destructive. When the new shoots reach a height of 45 inches (which results generally in about three years), they are effectively out of the reach of sheep, so that from then on to timber maturity grazing by sheep may be permitted.

Another paper resulting from studies in the Manti National Forest is the one by SAMPSON and WEYL on range preservation and erosion control. Overgrazing in this region, especially by sheep, has resulted in such a serious

destruction of the vegetation carpet as to have given rise to further and more serious loss through erosion. The peak of this destruction has been in the spruce-fir basins, above 9000 ft., where slopes are steep and summer grazing is excellent. Deferred and rotation grazing are necessary to prevent the destruction of these areas for grazing purposes; once erosion has set in, grazing should be abandoned, and an attempt made to re-create good grazing conditions by terracing, planting, and the construction of dams.

In connection with these bulletins there may be mentioned one on the general principles underlying range management in the National Forests,[3] in which such topics are considered as the determination of the class of stock to which the range is best suited, grazing periods, grazing capacity, management of cattle on the range, management of sheep on the range, range reseeding, and timber protection. Very full lists of references are given.

The ecological study of pastures has been taken up also in foreign lands. The work of BEWS in South Africa has already been noted in these pages.[4] An interesting study of Scottish hill pastures has been made by SMITH.[5] A hill pasture is defined as an area that is uninclosed and unploughed. Sixty per cent of the area of Scotland, or 18,000 square miles, comes under this category, although much of this is unsuitable for grazing. The different plant associations of these lands are mentioned and characterized, and it is clearly brought out that each association represents a particular combination of climate, soil, and grazing animals. The improvement of pasture land is based on the fundamental principle that the herbage changes as the growth conditions change. The foundation of hill pasturage is in the alluvial and flush grasslands, where the vegetation is rich and palatable; these areas may be extended by irrigation, diversion of surface water, and drainage. Bracken (*Pteris aquilina*) land is flush grassland with a luxuriant growth of the bracken. This land makes excellent pasturage if the bracken is removed by cutting or by spraying with 5 per cent sulphuric acid. Heather (*Calluna*) land is valuable for sheep grazing, but it should be burned over every few years, to stimulate the increased development of palatable green shoots. Peaty lands may be improved by drainage or burning. Considerable areas are characterized by rough grasses of low grazing value, notable among which are *Nardus stricta* and *Molinia coerulea*. It is desirable to replace these by finer herbage, by flushing, or by diverting surface water.

Quite another sort of applied ecology is represented in a paper by COKER[6] on pisciculture. Plants are the chief oxygenators in confined ponds, and are

[3] JARDINE, JAMES T., and ANDERSON, MARK, Range management on the National Forests. Bull. 790, U.S. Dept. Agric. pp. 98. *pls.* 32. *figs.* 4. 1919.

[4] BOT. GAZ. **67**:370. 1919.

[5] SMITH, W. G., The improvement of hill pasture. Reprint from Scottish Jour. Agric. pp. 8. 1918.

[6] COKER, R. E., Principles and problems of fish culture in ponds. Scientific Monthly **7**:120–129. *figs.* 2. 1918.

therefore of fundamental importance in fish culture. Although little is known yet as to which plant species are best for oxygenation, it is probable that evergreen species with finely divided leaves are the most satisfactory. It has long been known, of course, that plants are the basis of all fish food, but we are only just beginning to determine which species have the greater food values. Another thing of importance is the determination of the optimum association of species in a pond.—H. C. COWLES.

Cytology of Synchytrium and Urophlyctis.—Within a year considerable light has been shed on the puzzling problems of cytomorphology in the Chytridiales by reinvestigations of *Synchytrium* (*Chrysophlyctis*) *endobioticum* and *Urophlyctis alfalfae*. The careful and thorough studies of Miss CURTIS[7] on *Synchytrium* and of JONES and DRECHSLER[8] on *Urophlyctis* deserve particular notice. The most noteworthy results of Miss CURTIS' study of *Synchytrium* are the establishment of the occurrence of gametic fusions in the life cycle and the demonstration that a prosorus is regularly antecedent to the development of the sporangial sorus, the contents of this body passing into the host cell where segmentation into sporangia and production of zoospores take place. During the development of the prosorus from the infecting zoospore a series of nucleolar discharges of chromatin occurs, and the five chromosomes originate also from the nucleolus; but all divisions from the primary nucleus to the zoospore primordia are typically mitotic. The asexual or sexual nature of the motile cells terminating this series appears to depend on the availability or lack of water during maturation; if water becomes tardily available simultaneous germination of a number of sporangia occurs and their zoospores pair, probably exogamously. Unpaired zoospores and zygotes penetrate growing parts of potato plants; the former reproduce the prosorus phase, but the zygotes develop into resting sporangia. In the production of the latter no form of mitotic division was observed. Chromatic granules appear in the cytoplasm following nucleolar discharges, and after a further loss of chromatin (a process homologized with reduction) the granules become zoospore primordia. The existence of sexual fusions between facultative gametes is hypothecated for all Synchytriaceae which produce true resting spores. The validity of *Chrysophlyctis* is rejected, and the writer prefers the broader generic name *Synchytrium* to *Pycnochytrium*, to which the organism in all respects conforms.

The absence of mitosis in the development of the resting sporangium and the conception of nucleolar gemmation taking the place of meiotic divisions

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[7] CURTIS, K. M., The life history and cytology of *Synchytrium endobioticum* (Schilb.) Perc., the cause of wart disease in potato. Phil. Trans. Roy. Soc. London. B **210**:409–478. *pls. 12–16*. 1921.

[8] JONES, F. R., and DRECHSLER, CHARLES, Crown wart of alfalfa caused by *Urophlyctis alfalfae*. Jour. Agric. Res. **20**:295–324. *pls. 47–56*. 1920.

will still be unsatisfactory to cytologists who hope to standardize the essentials of nuclear behavior practically throughout the plant realm; and the conviction will persist that imperfect fixation within the resistant walls of the resting body has masked the appearance of mitotic divisions conforming to those of the prosorus in this species, of the resting sporangium in *S. decipiens* and *S. puerariae*, of *Rhodochytrium*, and others.

This work affords no support to the view advanced by ORTON[9] and KERN that the "primordial sphere" in *Synchytrium* is a chimera composed of a parasitic plasmodium enveloping an almost unmodified host nucleus. Figures of the type on which this view is based are interpreted as resulting from multiple infections, by which a number of zoospores come to lie about a single host nucleus. Subsequent divisions of the host cell distribute the supernumerary spores, leaving usually only one in each host cell. The reviewer, however, has observed two and even three cysts within one host cell in all stages of development up to resting sporangia. Furthermore, a series of preparations is readily obtained showing that, contrary to the view of ORTON and KERN, the primary nucleus of the cyst is the direct outgrowth of the zoospore nucleus, the host cell nucleus being crowded off to one side of the cyst, where it finally disintegrates.

WILSON[10] has published a more detailed account of the work on which his preliminary paper[11] on *Urophlyctis* was based, but the conclusions of both are identical. The direct functioning of the resting body as a sporangium, and the production of the resting "spores" in lysigenous cavities developed in the host tissues by a parasitic plasmodium are maintained.

SCOTT[12] found that the resting spores germinate by the proliferation of one to fifteen sporangia through pores of which the zoospores escape. JONES's and DRECHSLER's limited observations on germination are in agreement with the latter. As for the accounts of cytological details and life cycle of the pathogen, it seems evident that JONES and DRECHSLER have made their observations upon very different material and probably a different organism from that studied by WILSON. Judgment as to which is actually the crown wart disease of alfalfa and which is *Urophlyctis alfalfae*, if that name is to survive, must remain temporarily suspended, but the fine preparations of JONES and DRECHSLER obtained by dissecting the parasite from infected tissues and showing in detail the relations of turbinate cells, hyphae, resting spores, and haustoria leave no doubt that the organism which is the type for *Urophlyctis* is the one they studied. On the other hand, WILSON has made

[9] ORTON, C. R., and KERN, F. D., The potato wart disease. Penn. State College Agric. Exp. Sta. Bull. 156. pp. 16. *figs 4*. 1919.

[10] WILSON, O. T., Crown-gall of alfalfa. BOT. GAZ. **70**:51–68. *pls. 7–10*. 1920.

[11] ———, The crown-gall of alfalfa. Science **41**:797. 1915.

[12] SCOTT, C. E., A preliminary note on the germination of *Urophlyctis alfalfae*. Science **52**:225–226. 1920.

the association between resting spores and plasmodium on the basis of similarity of contents. The plasmodium may well be a secondary parasite. The existtence of an antheridial-oogonial sexual apparatus in *Urophlyctis* is definitely disproved, but WILSON's description of fusion between unlike zoospores must await confirmation.—FREEMAN WEISS.

Taxonomic notes.—HOCHREUTINER[13], in studying the Andean genus *Cristaria* (Malvaceae), has established two new subgenera (*Septaria* and *Aseptaria*), each including two new sections, besides describing several new species. In *Bakeridesia* also two new subgenera (*Monopteron* and *Dipteron*) are described, and one (*Pseudabutilastrum*) in *Malvastrum*.

DUNN[14] has described a new genus of Dipterocarpaceae (*Dioticarpus*) from Southern India. It is a valuable timber tree closely related to *Balanocarpus*.

WILDEMAN[15] has discussed various representatives of the African flora. *Clerodendron* (Verbenaceae) is represented by 31 species, 8 of which are described as new. *Acioa* (an African genus of Rosaceae) is credited with 37 species, 15 of which are new. A number of genera of Leguminosae are presented, including 23 new species distributed among 10 genera.

MOORE[16] has published the result of a study of the Australian collections at the British Museum, describing 89 new species in various families, and also a new genus (*Leptospermopsis*) of Myrtaceae.

DOP[17] has published 13 new species of *Clerodendron* (Verbenaceae) from Indo-China.

GAGNEPAIN[18] has published four new genera of Compositae from the Orient, as follows: *Camchaya*, *Iodocephalus*, and *Thorelia*, all belonging to Vernonieae, and *Colobogyne*, belonging to Coreopsidae.—J. M. C.

Welwitschia mirabilis.—When the third edition of *Morphology of Gymnosperms* by COULTER and CHAMBERLAIN was published in 1917, an important investigation of the floral structures of *Welwitschia* was overlooked. CHURCH[19]

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[13] HOCHREUTINER, B. P. G., Notes sur les genres *Cristaria*, *Bakeridesia*, *Malvastrum*. Ann. Conserv. Jard. Bot. Geneve **21**:405–428. 1920.

[14] Decades Kewenses: C.–CI. Kew Bull. 1920: no. 10. 1920.

[15] WILDEMAN, É. DE, Notes sur quelques espèces Africaines du genre *Clerodendron*. Bull. Jard. Bot. Bruxelles **7**:161–270. 1920.

[16] MOORE, S. LEM., A contribution to the flora of Australia. Jour. Linn. Soc. **45**:159–220. *pls. 11, 12.* 1920.

[17] DOP, PAUL, *Clerodendron* nouveaux de l'Indochine de l'herbier du muséum. Notulae Syst. Herb. Mus. Paris **4**:7–14. 1920.

[18] GAGNEPAIN, F., Quatre genres nouveaux de Composees. Notulae Syst. Herb. Mus. Paris **4**:14–19. 1920.

[19] CHURCH, A. H., On the floral mechanism of *Welwitschia mirabilis* Hooker. Phil. Trans. Roy. Soc. London **205**:115–151. *pls. 9–13.* 1914.

secured a very complete series of stages in the organogeny of both staminate and ovulate flowers from material furnished by PEARSON. The illustrations are so carefully drawn and the stages so close together, that one can study the problem for himself, from the first divergence in the topography of the staminate and ovulate flowers, up to the condition at the time of pollination. The facts of development are made still more valuable by detailed descriptions which prevent any misinterpretation of the figures.

When it comes to conclusions, however, each one will probably have his own theories in regard to the plant which so thoroughly deserves its specific name. That the ancestral flowers were functionally bisporangiate, all students of comparative morphology must agree. The evidence in favor of insect pollination is also rather complete. CHURCH does not believe that the evidence supports the contention that the "perianth" consists of decussate bracts. He believes that the reductions which have brought about a dioecious condition from an orginally bisporangiate flower are of the same type as those known in *Cycadeoidea* and *Williamsomia*, but that no relationship is involved in the similarity. He also fails to see any relationship to the flowers of Angiosperms, the resemblances being merely a "parallel progression of physiological mechanism devoted to seed production."—C. J. CHAMBERLAIN.

Myrmecophilous plants.—CHODAT and CARISSO[20] have found that in certain plants the relationship of the symbiotic ants is a secondary matter, the excrescences which they inhabit being really galls caused by hymenopterous larvae. All stages in the gall formation, from the deposition of the egg to the escape of the larva leaving a hole for the entry of the ants, were found in several South American species of *Cordia* (Boraginaceae) and in *Acacia Cavenia*. It is also pointed out that the symbiosis could not be regarded, as heretofore, as a protection against leaf-cutting ants, since the inhabitants of the galls on *Cordia* are themselves leaf-cutters, and their "ant gardens" within the galls are composed of bits of leaves and flowers which they have cut off and brought in.—GEO. D. FULLER.

Umbelliferous cushion plants.—Two closely related umbelliferous genera, *Azorella* and *Bolax*, are notable for their compact cushion habit. They occur in the high Andes, in Patagonia, and in the subantarctic portions of South America. HAUMAN[21] has reviewed the 24 species occurring in Argentine, giving ecological and taxonomic notes and describing one new species, *A. yareta*. The vegetation of the celebrated "balsam bogs" of Tierra del Fuego has *Bolax gummifera* as its characteristic species. A key has been constructed for the determination of the species and a very complete bibliography given.—GEO. D. FULLER.

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[20] CHODAT, R., and CARISSO, LUIS, Une nouvelle théorie de la myrmécophilie Compt. Rend. Soc. Phys. et Hist. Nat. Genève. **37**:9–12. 1920.

[21] HAUMAN, LUCIEN, Notes sur les espèces Argentine des genres *Azorella* et *Bolax*, Rev. Soc. Arg. Ciens. Nat. **4**:468–500. *figs.* 7. 1919.

GENERAL INDEX

Classified entries will be found under Contributors and Reviewers. New names and names of new genera, species, and varieties are printed in **bold-face** type; synonyms in *italic*.

A

Accessory foods for plants 247
Acer Negundo, diameter growth in 454
Acid soils, plants of 244
Adams, J. F. 131
African flora 471
After-ripening and germination of Juniperus seeds 32
Algae, ecology of 336; marine, of Beaufort 336; subterranean flora 78
Alpine adaptations 405
Aluminum and soil acidity 159
Alway, F. J., work of 80
Andersen, Emma N., work of 336
Anderson, M., work of 468
Angiosperms, correlations in herbaceous 1; Gnetalean vessels of 438
Anisantherina 240
Anthony, S., work of 77
Apogamy in Osmunda 79
Apples, odor constituents of 78
Arthur, J. C., work of 241
Arthur, J. M. 155
Artschwager, E. 400
Aseptaria 471
Atmometer, non-absorbing mounting 80
Australian flora 471
Awn and barley yield 77

B

Bacterial diseases of plants 401
Bailey, I. W. 334; work of 408
Bailey, L. H., work of 79
Ball, C. R. 426
Barley yield 77
Barratt, Kate, work of 335
Bembicidium 240
Bergman, H. F., work of 80
Berry, E. W., "Paleobotany" 238
Birch, experimental investigations on 220
Blackman, V. H., work of 246
Blakeslee, A. F. 75
Bliss, Mary C. 314
Blister rusts, gametophytic development of 131
Bonnier, G., work of 405
Bottomley, W. B., work of 247
Brause, G., work of 79
Britton, N. L., work of 240
Brown, Elizabeth Dorothy Wuist, work of 79
Brown, Isabel M. P., work of 335
Buchanan, R. E. 401
Burgeff, H., work of 75
Burt, E. A., work of 241

C

Calcium 76
Calymperaceae 240
Cambium, studies of 408
Camchaya 471
Cănizatesia 240
Carisso, L., work of 472
Caryophyllaceae, arctic 77
Ceratophorum ulmicolum 190
Chaetocladium and Mucor 75
Chamberlain, C. J. 408, 471
Cheilophyllum 240
Chestnut, V. K., work of 78
Chloroiodide of zinc in plant histology 400
Choate, Helen A. 409
Chodat, R., work of 472
Church, A. H., work of 471
Clark, W. M., "The determination of hydrogen ions" 155
Clerodendron in Indo-China 471
Coker, R. E., work of 468
Colobogyne 471
Colombia, Scrophulariaceae of 241
Congo, flora of 242
Conifer grafting 248
Contributors: Adams, J. F. 131; Arthur, J. M. 155; Artschwager, E. 400; Bailey, I. W. 334; Ball, C. R. 426; Blakeslee, A. F. 75; Bliss, Mary C. 314; Buchanan, R. E. 401; Chamberlain, C. J. 408, 471; Choate, Helen A. 409; Coulter, J. M. 79, 80, 239, 240, 336, 402, 408, 471; Cowles, H. C. 466; Cribbs, J. E. 289; Crocker, W. 76, 77,

78, 80, 157, 159, 160, 246, 247, 248; Eaton, S. V. 156; Fuller, G. D. 77, 80, 157, 160, 242, 244, 245, 246, 248, 334, 335, 336, 402, 403, 405, 407, 472; Gardner, W. A. 249; Hasselbring, H. 327; Haupt, A. W. 61, 446; Holm, T. 236; Jeffrey, E. C. 1; Johnson, D. S. 331; Jurica, H. S. 138; Karrer, Joanne 78; Korstian, C. F. 454; Line, J. 245; MacDuffie, R. C. 438; Macpherson, Gertrude E., 392; Miles, L. E. 161; Newcombe, F. C. 152; Noé, A. C. 238; Pack, D. A. 32; Sax, K. 399; Schaffner, J. H. 197; Schertz, F. M. 81; Seward, A. C. 462; Spessard, E. A. 406; Strausbaugh, P. D. 337; Torrey, R. E. 1; Tuttle, Gwynethe M. 146; Walker, Elda R. 378; Weiss, F. 469; Wells, B. W. 358; Whitaker, Edith S. 220
Convolvulus, development in 392
Coryneliaceae 241
Coryneum tumoricolum 191
Cotema 240
Coulter, J. M. 79, 80, 239, 240, 336, 402, 408, 471
Coville, F. V., work of 160
Cowles, H. C. 466
Craig, R. D., work of 242
Cribbs, J. E. 289
Crocker, W. 76, 77, 78, 80, 157, 159, 160, 246, 247, 248
Crown gall of alfalfa 245
Curtis, K. M., work of 469
Cuscuta, development in 392
Cushion plants 472
Cylindrosporium ulmicolum 190

D

Dimorphocladium 240
Dioticarpus 471
Dipsacus, development of head and flower 138
Dipteron 471
Dodder, development in 392
Dop, P., work of 471
Dormancy, and hardiness in plum 337; in trees 160
Douglas fir forests, reproduction of 242
Doyle, J. D., work of 408
Drechsler, C., work of 469

E

Eaton, S. V. 156
Ecology, applied 466; a new journal of 335; concepts and nomenclature 403
Elm, leaf spots of 161
Equisetum, anatomy of 334; laevigatum, gametophytes of 378
Eupatorium, Bolivian species of 242
Excipula ulmicola 191

F

Ferns of Papua 79
Feuer, B., work of 80
Fitzpatrick, H. M., work of 241
Fuller, G. D. 77, 80, 157, 160, 242, 244, 245, 246, 248, 334, 335, 336, 402, 403, 405, 407, 472

G

Gagnepain, F., work of 471
Galløe, O., "The lichen flora and lichen vegetation of Iceland" 239
Gametophytes of Equisetum laevigatum 378
Gardner, W. A. 249
Gentes Herbarum 79
Geography of plants 402
Germination, and after-ripening of Juniperus seeds 32; chemical changes in wheat 409; effect of light on 249
Gibbs, L. S., work of 157
Gloeosporium **ulmeum** 182; **ulmicolum** 185
Gnetalean vessels in Angiosperms 438
Gnomonia ulmea 162

H

Haas, P., "An introduction to the chemistry of plant products" 156
Hardy, M. E., "Geography of plants" 402
Harlan, H. V., work of 77
Harris, F. S., "Soil alkali" 157
Harris, W., biographical sketch of 331
Hasselbring, H. 327
Hauman, L., work of 472
Haupt, A. W. 61, 446
Hemp, sexual expression in 197
Hill, T. G., "An introduction to the chemistry of plant products" 156
Hitchcock, A. S., work of 241
Hochreutiner, B. P. G., work of 471
Hofmann, J. V., work of 243
Holden, H. S., work of 79
Holloway, J. E., work of 406
Holm, T. 236
Hoyt, W. D., work of 336
Humidity and irrigation 248, 336
Hydrogen ion determination 155

I

Iceland, botany of 239
Iodocephalus 471
Irrigation and humidity 248, 336

J

Jardine, J. T., work of 468
Jeffrey, E. C. 1
Johnson, D. S. 331
Jones, F. R., work of 469
Juniperus, after-ripening and germination of seeds 32
Jurica, H. S. 138

K

Karrer, Joanne 78
Kern, F. D., work of 470
Koketsu, R., work of 407
Korstian, C. F. 454

L

Larix, morphology of 408
Leaf spots of elm 161
Leaves, mottling of 81
Leptospermopsis 471
Light, effect on germination 249
Line, J. 245
Livingston, B. E., work of 80, 407
Lycopodium 406

M

MacDuffie, R. C. 438
Macoun, John, biographical sketch of 236
Macpherson, Gertrude E. 392
McCool, M. M., work of 160
McGregor, E. A., work of 248, 336
McLean, F. T., work of 247
Magnus, P., work of 246
Martin, J. N., "Botany with agricultural applications" 402
Maxon, W. R., work of 242
Melasmia ulmicola 191
Mexican trees and shrubs 241
Meyer, F. J., work of 334
Michaelis, L., work of 155
Miles, L. E. 161
Millar, C. E., work of 160
Mirasol, J. J., work of 159
Monocardia 241
Monopteron 471
Moore, G. T., work of 78
Moore, S. LeM., work of 471
Morning glory, development in 392
Mottling of leaves 81
Mucor and Chaetocladium 75
Munger, T. T., work of 242
Mycosphaerella ulmi 189
Myrmecophilous plants 472

N

Naiadothrix 240
Nathorst, A. G., biographical sketch of 462
Neller, J. R., work of 76
Newcombe, F. C. 152
Nichols, G. E., work of 245
Nitrites and nitrates in plants 248
Noé, A. C. 238
North American flora 240, 408

O

Oak, experimental investigations on 220
Orton, C. R., work of 470
Osmunda, apogamy in 79
Østrup, E., "Fresh-water diatoms from Iceland" 239

P

Pack, D. A. 32
Paleobotany, textbooks of 238
Paniceae 241
Papua, ferns of 79
Parker, F. W., work of 77
Pavillard, J., work of 403
Peat soils 80
Pemberton, C. C., work of 160
Pennell, F. W., work of 241
Pfeffer, Wilhelm, biographical sketch of 152
Phoma cincta 191
Photosynthesis, rate of 247
Phyllosticta confertissima 191; ulmicola 190
Picea Parryana, diameter growth in 454
Plant products, chemistry of 156
Plum, dormancy and hardiness in 337
Potonié, H., "Lehrbuch der Paläobotanik" 238
Power, F. B., work of 78
Practical botany 402
Pseudabutilastrum 471

R

Radio-active material 246
Ramaley, F., work of 246
Ramsdenia 240
Raunkiaer, C., work of 404
Reboulia, embryogeny and sporogenesis in 446; gametophyte and sex organs of 61
Reserve food in vegetative tissues 146
Reviews: Berry's "Paleobotany" 238; Clark's "The determination of hydrogen ions" 155; Gallœ's "The lichen flora and lichen vegetation of Iceland"

239; Haas' "An introduction to the chemistry of plant products" 156; Hardy's "Geography of plants" 402; Harris's "Soil alkali" 157; Hill's "An introduction to the chemistry of plant products" 156; Martin's "Botany with agricultural applications" 402; Østrup's "Fresh-water diatoms from Iceland" 239; Potonié's "Lehrbuch der Paläobotanik" 238; Scott's "Studies in fossil botany" 238; Smith's "Bacterial diseases of plants" 401
Rhytisma ulmi 191
Robinson, B. L., work of 242
Roigia 240
Romell, Lars-Gunnar, work of 248, 404

S

Salix Farrae **Walpolei** 435; lasiolepis **Bakeri** 436; lutea **famelica** 426; lutea **ligulifolia** 428; lutea **platyphylla** 430; **monochroma** 431
Sampson, A. W., work of 466
Sax, K. 399
Schaffner, J. H. 197
Schertz, F. M. 81
Schroeter, J., work of 246
Scott, C. E., work of 470
Scott, D. H., "Studies in fossil botany" 238
Seacoast vegetation 245
Seedling anatomy 79
Seeds, device for weighing 399; effect of light on germination 249
Selaginella 242
Septaria 471
Septogloeum profusum 190
Seward, A. C. 462
Sexual expression in hemp 197
Shedd, O. M., work of 76
Shull, C. A., work of 407
Silvinula 240
Smith, E. F., "Bacterial diseases of plants" 401
Smith, W. G., work of 468
Soil, acidity and aluminum 159; alkali 157; soluble substances in 160
Spessard, E. A. 406
Sphaereupatorium 242
Sphaeria apertiuscula 191
Standley, P. C., work of 241
Stoma, internal 80
Strausbaugh, P. D. 337
Strowd, W. H., work of 248
Stumps, living 160
Subalpine lake shore vegetation 246
Subterranean algal flora 78
Synchytrium, cytology of 469
Systremma ulmi 186

T

Tanner, F. R., work of 80
Tansley, A. G., work of 334, 403
Tasmanian mountains, vegetation of 157
Thelephoraceae 241
Thermoregulator 327
Thone, F., work of 80
Thorelia 471
Tilia americana, ecology of 289
Torrey, R. E. 1
Transpiration, comparative studies of 289
Trees, dormancy in 160
Truog, E., work of 77
Tuttle, Gwynethe M. 146

U

Ultra-violet light and yeast 80
Unanuea 241
Uredineae 241
Urophlyctis, cytology of 469

V

Vessel in seed plants 314
Von Lagerheim, G., work of 246

W

Walker, Elda R. 378
Warming, E., work of 77
Weiss, F. 469
Wells, B. W. 358
Welwitschia mirabilis 471
Weyl, L. H., work of 466
Wheat, chemical changes in germination 409
Wherry, E. T., work of 244
Whitaker, Edith S. 220
Whitford, H. M., work of 242
Wildeman, E. de, work of 242, 471
Williams, R. S., work of 240
Wilting coefficient studies 407

Y

Yeast, and ultra-violet light 80

Z

Zoocecidia, evolution of 358

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Professor of Botany in the University of Chicago

This book (third edition, completely revised) contains directions for collecting and preparing plant material for microscopic investigation. Killing and fixing, freehand sectioning, the paraffin method, the Venetian turpentine method, the celloidin method, and the glycerin method are treated in detail, and chapters on making photo-micrographs and lantern slides have been added. In later chapters specific directions are given for making such preparations as are needed in a study of the plant kingdom from the algae up to the flowering plants. Ten years' experience with the Venetian turpentine method has brought it to a high degree of efficiency; the paraffin method has been greatly improved; the notes on staining have kept pace with cytological research, and the directions for finding material are more extensive.

The book may be used in classes under an instructor, but the directions are so explicit that students working alone should soon learn to make first-class preparations.

With the exception of the sections on the glycerin and celloidin methods, this third edition is practically a new book.

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